CRYPTIC DENSITY DEPENDENCE: EFFECTS OF COVARIATION BETWEEN DENSITY AND SITE QUALITY IN REEF FISH

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Abstract. The importance and strength of density dependence continues to engender debate because of its central importance to population dynamics and regulation. Here, we show how confounding effects of site quality can mask strong effects of density dependence. In particular, we explore spatiotemporal variation and covariation among (1) densities of newly settled coral reef fish (*Thalassoma hardwicke*), (2) environmental characteristics, and (3) the strength of density-dependent mortality. Environmental features of patch reefs were spatially and temporally variable and influenced density-dependent survival. Higher-quality sites (i.e., reefs possessing features that yield greater numbers of recruits at any given settlement level) received greater settlement, and this relationship masked the operation of density dependence when variation in quality among sites (or times) was not distinguished (a common approach in many observational studies of density dependence). Our work illustrates how spatiotemporal covariation in settlement density and site quality can obscure patterns of density dependence at larger scales, contributing to a phenomenon we call "cryptic density dependence." Acknowledging patterns and consequences of covariance may alter the way we study population dynamics, especially of marine organisms, where the link between processes that affect settlement and post-settlement survival remains relatively poorly understood.

Key words: density independence; density-dependent survival; environmental variability; post-settlement mortality; recruitment; regulation; settlement; site quality; Thalassoma hardwicke.

INTRODUCTION

The factors that drive spatial and temporal variability in population density and structure have long attracted the attention of ecologists (Nicholson 1933, Andrewartha and Birch 1954). Much of this focus has centered on the strength and importance of density dependence, with some studies leading to the conclusion that density dependence plays a minor role and others suggesting a predominant role. Although these differences may be real, in some cases, the discrepancies may result from differences in the approaches used to quantify density dependence (e.g., Murdoch 1994, Turchin 1995, Wilson and Osenberg 2002). These issues are particularly apparent in studies of marine systems, where debate continues over the relative magnitude of variation in population dynamics and the processes that drive the observed variation (Caley et al. 1996, Schmitt et al. 1999).

Most marine reef organisms have a bipartite life history, consisting of a pelagic larval stage followed by a relatively sedentary benthic stage (Sale 1980, Booth and Brosnan 1995). The two life stages are coupled through a transition called settlement, in which larvae are delivered to potential sites through a combination of currents (e.g., Cowen and Castro 1994) and larval

behavior (e.g., Stobutzki 1997). Although both settlement and post-settlement survival affect the abundance of benthic populations (e.g., Doherty and Fowler 1994, Forrester 1995, Hixon and Carr 1997, Steele 1997, Schmitt et al. 1999, Shima 2001*a, b,* Doherty 2002), disproportionate attention has been given to variability in settlement as a driver for variation in abundance of older life stages, probably because variability in settlement is easy to measure and density dependence is typically viewed as homogenizing force. However, many studies have linked variation in a variety of demographic rates (e.g., settlement and survival) of benthic marine organisms to specific environmental attributes, such as substrate composition and densities of competitors and predators (reviewed in Jones 1991). As a result, we expect that spatial variability in settlement and environmental characteristics can create a mosaic of patches with varying strengths of density-dependent and density-independent processes (e.g., Shima 1999). Yet our sense of the importance of variability in density dependence may be misinformed because most studies fail to estimate variability in the strength of density dependence or its covariates (Osenberg et al., *in press*).

By emphasizing spatial variation in the strengths of post-settlement processes within a context of variable settlement, we are forced to conceptually link, and explicitly study patterns of covariance between these two

sources of variation for older life stages. Patterns of covariance are particularly informative because they can mask the importance of processes that determine patterns of abundance (e.g., Beukers and Jones 1997, Shima 2001*a, b,* Wilson and Osenberg 2002), and perhaps more importantly, because they can give rise to diverse dynamics that alter the way we conceptualize the functioning of marine systems (e.g., Chesson 1998), in particular the role and importance of density dependence.

Here we developed an approach to explore the effect of spatial variation in environmental factors on site quality and the strength of density dependence, and investigated some of the consequences of spatial co-variation in site quality and settlement intensity. Specifically, we tested the conceptual model proposed by Wilson and Osenberg (2002) to explain the dramatic differences in effects of density that they detected in an experimental study compared to an observational study. Wilson and Osenberg argued that their observational study underestimated the effect of density dependence because of the confounding effects of site quality and the underlying association between settlement intensity and site quality: sites that naturally received more settlers were better able to support those fish, thus obscuring the true effects of density on survival. We term this phenomenon "cryptic density dependence." Their experimental study, which relied on random assignment of treatments to sites, decoupled this confounding influence and therefore revealed strong effects of density. There were, however, several alternative explanations for the disparity between the experimental and observational results discussed by Wilson and Osenberg, including the possibility that handling led to the stronger density dependence in the experimental study. Our approach, based entirely on observational data, avoids this potential confounding influence and therefore provides a strong test of their model. Furthermore, our results underscore the need to consider spatiotemporal variation in quality when quantifying density dependence.

METHODS

A framework to evaluate site quality and the strength of density dependence

We model the relationship between the per capita survival of recently settled fish and the density of the cohort as

$$dN/Ndt = -\alpha - \beta N \qquad (1)$$

where N is the density of fish in the cohort, β is the density-dependent mortality rate (measured per conspecific), and α is the density-independent mortality rate. Both α and β take on values >0 (unless mortality decreases with density, in which case $\beta < 0$). Eq. 1 can be integrated to yield the Beverton–Holt recruitment function (Beverton and Holt 1957):

$$N_t = \frac{e^{-\alpha t}N_0}{1 + \dfrac{\beta(1 - e^{-\alpha t})N_0}{\alpha}} \qquad (2)$$

which describes the relationship between the number of surviving juveniles (N_t) and the initial number of settlers (N_0). Eq. 2 results by assuming that density-dependent mortality changes instantaneously as density changes. If, in contrast, the intensity of density dependence is set by initial density and does not change as numbers in the cohort decline, the result is a Ricker recruitment function (Ricker 1954):

$$N_t = N_0 a e^{-\beta N_0 t} \qquad (3)$$

where $a = e^{-\alpha t}$.

In principal, α and/or β in these expressions may be constant in space and time, or they may vary as functions of environmental characteristics. If they vary, some sites will have characteristics associated with lower mortality rates (via α or β), and hence will be of higher "quality." For example, if the variation in factors that influence β is large among sites (relative to those that affect α), then overall variation in site quality may be produced primarily by variation in β. The "best" sites, by definition, will harbor individuals that experience weaker per capita effects of conspecifics, and will yield the greatest numbers of individuals at time t for any particular level of settlement. We applied this approach to (1) describe spatial and temporal variability in environmental characteristics, (2) quantify how variation in α and β, and hence site quality, correlates with the environmental variation, (3) quantify the covariation between site quality and settlement intensity, and (4) examine how this covariation affects the detection of density dependence.

Study system and data collection

Fieldwork was conducted in the lagoons surrounding the island of Moorea, French Polynesia (17°30′ S, 149°50′ W) and focused on the six bar wrasse (*Thalassoma hardwicke*; see Plate 1). Six bar wrasse larvae develop in the pelagic environment for ~47 d (Victor 1986) before settling to reef habitat. Because settlement occurs during discrete lunar periods, and because settlers have different morphology and behavior than older fishes, accurate estimates of daily settlement and cohort survival are easily obtained (for details see Shima 1999, 2001*a, b*). In addition, settlers and juveniles utilize a broad range of habitats (Shima 2001*b*), albeit with unknown demographic consequences.

We made 480 observations of settlement events (i.e., pulses of settlement to individual sites) and monitored survivorship of six bar wrasse cohorts formed by these events. These were made during and after three periods of heavy settlement in May 1996, May 1997, and June 1997, using 192 patch reefs. Patch reefs were originally selected in two categories: (1) those with damselfish

PLATE 1. Adult six bar wrasse (*Thalassoma hardwicke*) on Moorea, French Polynesia. Shown are a group of adults preying upon the eggs of a territorial damselfish, *Stegastes nigricans*. These adult wrasse represent the product of recruitment. (Photo credit: J. Shima.)

(*Stegastes nigricans*) territories composed primarily of algal turf (*n* = 96 reefs, surveyed during all three settlement periods), or (2) those lacking damselfish territories and composed primarily of living coral (*Porites lobata*; *n* = 96 reefs, surveyed during May and June of 1997 only). Other than this difference, all reefs were selected to be relatively similar in size, rugosity, and distance from nearest neighbors (described in Shima 2001*b*). Reefs were censused daily during periods of heavy settlement, and every third day during other times for densities of (1) settlers (and these cohorts were then followed through time), (2) older conspecifics, (3) heterospecific labrids and scarids, and (4) resident piscivores. Censuses were continued for a period of 90 d following each settlement event. At the end of the study in each year, we recorded the densities and sizes (aerial coverage) of fine-branching corals (*Pocillopora* spp.) on each reef.

Environmental variability among sites and heterogeneity in α and β

We used a principal components analysis (PRINCOMP procedure in SAS version 8.02; SAS 1999) to summarize the observed environmental variation among reefs, and subsequently used the results of the principal components analysis (PCA) to model heterogeneity in α and β.

PCA.—The environmental variables used in the PCA were the time-averaged (over the 90-d post-settlement period specific to each focal cohort) density of potential competitors (older conspecifics, heterospecific labrids and scarids), and density of potential predators (resident piscivores), as well as refuge availability (i.e., *Pocillopora* coverage), and substrate type (algal turf or living coral). Each of these factors might influence, or otherwise be indicative of, site quality for newly settled wrasses. Densities and refuge availability were transformed using $\log_{10}(x + 0.1)$. Substrate type was coded

as a categorical variable: 1 for sites without damselfish territories (i.e., primarily *Porites*), and 2 for sites with damselfish territories (i.e., primarily algal turf). The first principal component accounted for 56.5% of the overall variance in the data set, and exhibited positive loadings for all variables, which were approximately equal in magnitude (all were between 0.65 and 0.82). We therefore used the first principal component as a description of the environment (and we give this the symbol E).

Estimation of α and β.—We examined whether the major source of environmental variability (i.e., E) was related to site quality, by contrasting a series of statistical models that described alternative relationships between the environment (i.e., E) and site quality (i.e., α and β). These models were constructed in a crossed fashion based upon (1) the form of the recruitment function (Beverton–Holt, Eq. 2 vs. Ricker, Eq. 3), (2) the relationship between β and E (independent: $\beta = 0$ or $\beta = \beta_0$; linearly related: $\beta = \beta_0 + \beta_E E$; or nonlinearly related: $\beta = \beta_0 /(1 + \beta_E E)$), and (3) the relationship between α and E (same possible forms as for β). This yielded a total of 32 ($2 \times 4 \times 4$) possible models, although four were redundant, so we evaluated 28 models. Parameters for each model were estimated using nonlinear regression (SAS NLIN procedure, method = Marquardt, constrained by the condition that $\alpha \leq 0$; SAS 1999). We then evaluated alternative models using Akaike's Information Criterion (AIC, Akaike 1992); the best model was the one with the smallest AIC.

Effects on the detection of density dependence

We compared system-wide estimates of density dependence using three approaches. First, we averaged the estimates of β from each settlement event obtained from the best model (see *Estimation of α and β*) to get a system-wide estimate of density dependence. We call this the "heterogeneous case," because local sites dif-

fered in β. We contrasted this result with two ''homogeneous'' cases, each of which assumed that α and β were invariant in space and time. The homogeneous cases are more typical of what is usually done in estimating patterns of density dependence using observational data. In the first of these homogeneous cases, we simply fit a single Beverton–Holt recruitment function to the 480 events. As demonstrated in the results, Beverton–Holt models generally outperformed Ricker models. In the second case, we aggregated the data, which is often done in field studies by sampling over larger spatial scales to reduce noise in the data set. We simulated this by combining data based on environmental traits, in part, because environmental features (and, hence, site quality) appear to have a spatial component when evaluated at a large scale (Shima 1999). We ranked sites by $E,$ sorted the 480 events into 24 groups (each consisting of 20 observations), summed the settlement and recruitment within these groups, and then fit a Beverton–Holt recruitment function these 24 estimates of N_t and N_0.

RESULTS

Demographic variation among reefs of differing quality

There was considerable variation in the performance of the statistical models describing the relationship between the environment and site quality. The Beverton–Holt function consistently outperformed the Ricker function. For example, in comparing each Beverton–Holt and Ricker pair (each with the same functional form for α and β), the Beverton–Holt model fit better in 11out of 12 comparisons (mean AIC_{Ricker} − $AIC_{Bev-Holt}$ = 25.6). All Beverton–Holt models with an underlying relationship between β and the environment (E), performed better than the model with α and β constant (the minimum difference in AIC was 37). Overall, the best model (based on the smallest AIC) was the one in which the relationship between N_t and N_0 was described by a Beverton–Holt recruitment function, with $\alpha = 0$ and β a nonlinear function of E:

$$N_t = \frac{N_0}{1 + \left(\dfrac{\beta_0}{(1 + \beta_E E)}\right)N_0 t} \tag{4}$$

where β_0 and β_E define the relationship between β and $E,$ with $\beta_0 = 0.0341$ (95% CI, ± 0.0035) and $\beta_E = 0.3148$ (±0.0602). Eq. 4 explained 45.5% of the variation in N_t across all 480 settlement events. However, because our 480 observations of settlement events included 132 observations of zero settlement (and, hence, zero recruitment), these observations were not informative in distinguishing among competing models. Therefore, we reevaluated the fit of the best model excluding these observations: r^2 decreased to 0.28, and confidence intervals for β_0 and β_E increased slightly
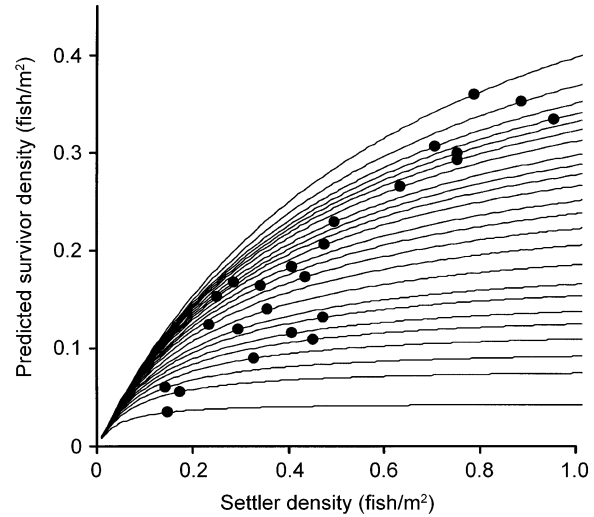

FIG. 1. Cryptic density-dependent survival of *Thalassoma hardwicke*. For presentation, 480 survivor settler events have been aggregated into 24 groups of 20 events, based on similarities in environmental characters. The figure presents fitted relationships (based on mean β within each group: see Eq. 4) between predicted density of survivors and initial density of settlers for patch reefs with similar environmental characters. Departure of the relationships from a linear relationship passing through the origin arises from the effect of density dependence. The curves that lie above others are characterized by weaker density dependence. Average settlement (and predicted recruitment) for each group is superimposed on each relationship (solid circles). Note that failure to discriminate variation in site quality would lead to a recruitment function that was approximately linear (i.e., leading to the erroneous inference that survival was density independent), despite underlying effects of density (i.e., a relationship fit to the points would be much more linear than the plotted relationships).

(to ±0.0042 and ±0.0709, respectively), due to the reduction in degrees of freedom.

We used a random effects ANOVA to partition variation in quality (i.e., β) to spatial (patch reef), temporal (settlement pulse), and spatiotemporal (error) variation (using the VARCOMP procedure in SAS 1999). Only 16% of the variation in β was attributable to main effects of patch reef or time. The remaining 84% of the variation was unexplained, suggesting that variation in quality is highly dynamic and can be interpreted as primarily spatiotemporal, with no consistent variation among patch reefs or settlement pulses. Overall, these results provide convincing evidence that there is spatiotemporal variation in the strength of density dependence, and, hence, what we call site quality.

Importantly, settlement was positively correlated with site quality (i.e., settlement intensity and β were negatively correlated: $P < 0.0001$, $n = 480$, $r = 0.39$), indicating that settlement was greatest to sites where density dependence was weakest (see Fig. 1). Although it is unclear what mechanisms produced this result (e.g., active habitat selection by larvae or physical transport processes: see Wilson and Osenberg 2002),
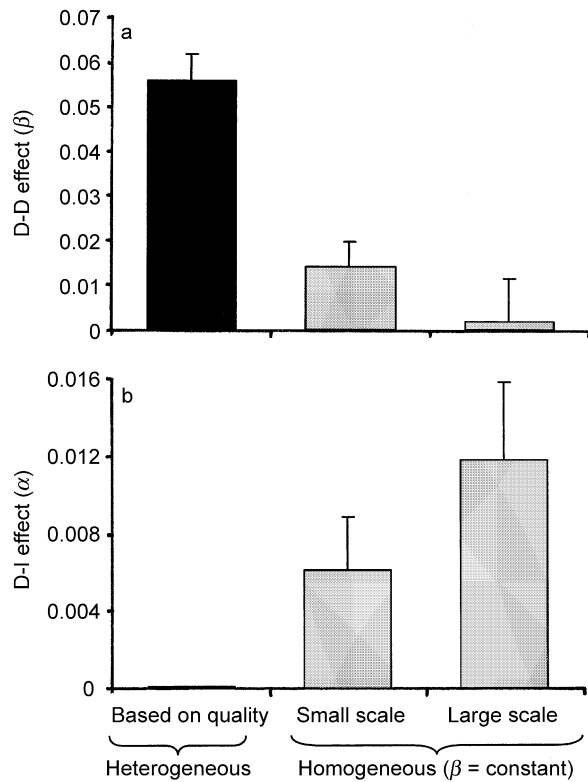
FIG. 2. Sensitivity of parameter estimation to variation in site quality. The figure presents parameter estimates (and upper bounds of symmetric 95% confidence intervals) for (a) density-dependent effects (per capita effects of conspecifics, β; D-D effect) and (b) density-independent effects (D-I mortality rate, α). Results for the heterogeneous case are based on the best model (evaluated using AIC) describing a relationship between environmental characters and the strength of density dependence (see Eq. 4). Results for the homogeneous cases (i.e., assuming a single fixed α and β) were obtained by fitting Eq. 2 to all 480 survivor settler events (small scale) or to 24 groupings of data based on aggregations of 20 observations (large scale). Units for β are square meters per fish per day ($m^2 \cdot [fish]^{-1} \cdot d^{-1}$); those for α are per day (d^{-1}).

the correlation has important implications for the detection of density dependence. Specifically, this combination of variation in site quality and the correlation between settlement and site quality gives rise to what we call cryptic density dependence, which we illustrate by comparing the above results with more standard analyses that ignore underlying variation in site quality (Fig. 1).

If the observed settlement events are used to estimate a single recruitment function, as is commonly done in the literature (e.g., Jones 1990, 1991, Doherty 1991, Doherty and Fowler 1994, Shima 2001a), the observed relationship between N_t and N_0 indicates much less severe density dependence than that found using the heterogeneous model (Fig. 2). Indeed, the average per capita effect of conspecifics assessed using our heterogeneous model ($\overline{\beta} = 0.0562$) was almost four-fold greater than estimated with the homogeneous model at

the smallest scale ($\beta = 0.0142$), and nearly 30-fold greater than obtained at a larger scale based on aggregated data ($\beta = 0.00193$, a value statistically indistinguishable from 0; Fig. 2a). Thus, the effect of density dependence was hidden by the underlying variation in site quality and the correlated patterns of settlement (see Fig. 1). Interestingly, the estimated effects of density-independent mortality (α) varied inversely with estimates of density-dependent mortality (β) obtained from these different approaches (Fig. 2b).

DISCUSSION

Our results show how environmental attributes of local sites can affect the strength of density dependence to create a mosaic of patches of variable quality. Patterns of settlement in our system positively covaried with β (the main component of site quality), and this produced an approximately linear relationship between survivors and settlers, despite the presence of strong, albeit spatially variable, effects of density. Linear relationships between densities of initial (N_0) and subsequent (N_t) life stages are typically interpreted as evidence for the absence of density dependence (reviewed in Doherty 1991). Thus, failure to distinguish variability in site quality may inhibit our ability to detect, and accurately quantify, density dependence, especially in systems where interactions occur on small spatial scales or within local neighborhoods.

We found the magnitude of cryptic density dependence in our data set to be particularly striking given that the reefs used in this study were selected a priori to *minimize* potential variation in quality (i.e., patch reefs were of similar size, rugosity, isolation, and limited to two substrate types). Our analyses suggest that failing to account for the observed heterogeneity in quality among sites underestimated the strength of density dependence by nearly 75% relative to the heterogeneous case. Aggregation of the data to simulate the sampling of our system over a larger spatial scale underestimated β by ~97%. Estimates of density independence varied in the opposite direction among the three approaches. Thus, the correlation between settlement and site quality could have led to the misassignment of effects of density into the density-independent term: e.g., based on the aggregated data set, the likely, but erroneous, conclusion would be that fish incurred a density-independent mortality rate of over 1% per day and that density had no effect on this rate. This raises the possibility that debate about the relative strength of density-dependent vs. density-independent processes might be attributable to variation in the approach (experiment vs. observational: Wilson and Osenberg 2002) or the similarity of the sites used in observational studies (and thus the strength of cryptic density dependence), and not the actual strength of density-dependent and density-independent processes. In addition, such large differences in parameter estimates also could have profound effects on predicted respons-

es of a population to environmental change or management strategies.

A principal components analysis allowed us to characterize variation in environmental attributes, facilitating estimates of α and β as functions of environmental characteristics. Our analyses revealed that ''good'' sites were those with more *Pocillopora* (a fine-branching coral), but less *Porites* (a mounding coral), and containing damselfish territories (and thus more algal turf). Branching corals and algae are used as shelter by young six bar wrasse, and thus might represent refuge from predators. The presence of territorial damselfish might also deter predators. Oddly, however, ''good'' sites also had high densities of potential competitors and predators. We speculate that a generic feature of site quality (e.g., shelter availability or current regimes) may increase general fish abundance, resulting in sites of high quality that simply support more fish. Additional manipulations of habitat attributes are be required to disentangle determinants of site quality.

Furthermore, we can only speculate on the mechanisms that may drive cryptic density dependence in our system, but we expect that (1) local hydrodynamics underlying both patterns of settlement and site quality and/or (2) active choices by settling larvae among sites of variable quality (e.g., achieving an ''ideal free distribution'', sensu Fretwell and Lucas 1970) contribute to this pattern (see also Wilson and Osenberg 2002). Previous observations and experiments suggest the likelihood of both processes driving cryptic density dependence for *T. hardwicke* (Shima 2001*b*).

Cryptic density dependence results from the positive correlation between settlement and site quality (Fig. 1). Although our data, and the likely mechanisms, involve positive correlations between settlement and site quality, other patterns are possible. For example, a negative correlation would lead to overestimates of density dependence. Furthermore, the strength of density dependence may never be unambiguously estimated using observational data. Here, we have shown how it can be underestimated with homogeneous models, but it is not clear to what extent the PCA captures all relevant environmental features that influence site quality; if not, then our heterogeneous model will yield underestimates of the strength of density dependence. Experimental manipulations remain the best approach to resolve this problem, although they are not feasible in all (or even most) systems. Interestingly, Shima (2001*a*) conducted experimental manipulations of density in this same system. The β estimated from those data was 0.12 m²·fish·d (approximately two-fold greater than estimated here, although the 95% condifence intervals are large: -0.09 to 0.34; Osenberg et al. 2002). Thus, it is unclear whether the estimates based on the observational data that incorporate environmental site variation capture most of the relevant variation in site quality.

The extent to which cryptic density dependence is a common feature of systems is currently unknown, owing to a lack of studies that quantify within-system variability in the strength of density dependence and its covariates. However, at least one other study (Wilson and Osenberg 2002) suggests similar patterns of covariance for small reef fishes (*Gobiosoma* spp.) in St. Croix, U.S. Virgin Islands. Wilson and Osenberg (2002) hypothesized that a mismatch in the strengths of density dependence estimated from experiments (with random assignment of treatments) and observational studies (lacking randomization) could be explained by confounding effects of site quality and an underlying association between settlement intensity and site quality in the latter. Our work from Moorea compliments the hypotheses posed by Wilson and Osenberg (2002). For example, Shima's (2001) experimental data yielded estimates of β that were ~10-fold greater than the observation data based on a homogeneous model. This 10-fold difference between experimental and observational data is similar to that found by Wilson and Osenberg (2002). Together, these studies emphasize the need to consider multiple demographic rates (e.g., settlement and post-settlement survival), and particularly how they covary with one another, to better understand sources of spatial variation that drive population dynamics, especially in open, marine systems.

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