

COMPENSATORY REPRODUCTION IN NORTHWESTERN HAWAIIAN ISLANDS LOBSTERS

BY

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ABSTRACT

Several related life-history attributes (size-specific fecundity, egg size, and body size at sexual maturity) were examined for Hawaiian spiny (*Panulirus marginatus*) and slipper (*Scyllarides squammosus*) lobsters sampled during the 1990s through 2001. Slippers were studied at Maro Reef, and spinys primarily at Necker Island bank. Size-specific fecundities of spinys were estimated at both reefs in 1991 and compared with respective estimates using lobsters collected a decade prior in 1979-81. Fecundities increased 16% on average (per female) between the two periods at Necker, where most commercial extraction had occurred, but did not change at Maro. An extended comparison was made using spinys collected from Necker in 1999; this documented a further 18% increase in fecundity and confirmed the prior suggestion that egg size is not a temporally labile trait in this species, at least at this bank. The cumulative one-third increase in observed fecundity was concurrent with a fivefold decrease in density based on lobster catch per trap-haul for the commercial fishery and research surveys. A companion study estimated size-specific fecundity and egg size for slippers at Maro. Other research demonstrated a decline in median body size at sexual maturity for spinys at Necker around the peak of the commercial trap fishery in the early 1990s that persisted at least through the 2001 research survey. Yet another study described a morphological metric (allometric pleopod-to-tail width relation) suitable for identifying body size at functional maturity of both species, which provides a previously lacking capability for slippers. These papers, whether directly or indirectly describing compensatory responses important to lobster management, together provide the reproductive parameter estimates that are necessary, but in themselves not sufficient, for the spatially structured assessments of lobster stocks in the Northwestern Hawaiian Islands (NWHI) that have recently been initiated.

INTRODUCTION

A NWHI lobster trap fishery developed in the late 1970s; by 1983 the fishery was well developed, generating annual catches of about 100,000-600,000 lobsters during the period from 1983-92 (DeMartini et al., 2003). Starting in 1998, the fishery, which prior to this had targeted the endemic Hawaiian spiny lobster almost exclusively, additionally

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targeted a species of non-endemic slipper lobster because of its increasing proportion in the lobster catch and declines in catch rates of spiny lobster. The fishery was closed in 2000 because of growing uncertainty regarding the population models used to assess stocks (DeMartini et al., 2003).

Evaluation of the status of lobster resources to date has been based on delay-difference models that rely on catch and effort data, adjusted by grossly estimated or assumed values of growth, recruitment, and mortality. Quantitative estimates of vital (birth-immigration, growth, mortality-emigration) rates, required as inputs to stage- (size- or age-) structured stock assessments, are outdated or lacking. Modern assessments of lobster stocks must incorporate density-dependent growth and reproduction; compensatory somatic growth, for example, has been described for many lobster stocks (Pollock, 1995a,b). The present depressed status of NWHI lobster stocks calls for a broad biological underpinning of management decisions and for a species-specific, spatially structured approach to future assessments of lobster stocks in the NWHI.

My objectives are to briefly review recent research on the reproductive life history of spiny and slipper lobsters in the NWHI, with emphasis on possible compensatory reproduction. I also note the types of information that are still lacking and needed before - spatially structured stock assessments can be made, and offer some suggestions for future research.

REPRODUCTIVE BIOLOGY OF NWHI LOBSTERS

The first study of NWHI lobster reproductive biology, conducted subsequent to the 2nd NWHI Symposium in 1984, was that of Polovina (1989) on spinys, then the major target species of the fishery. Polovina (1989) provided the first evidence suggesting a density-dependent response in life history characteristics—i.e., a 9-10% decline in body size at sexual maturity for female spinys between the pre-exploitation period in 1977 (Necker bank: 67.8 cm, Maro Reef: 74.8 cm carapace length CL) and an early peak period of the fishery in 1987 (60.8 and 68.2 cm CL, respectively; Fig. 1). Based on these specimen measurements, purportedly representative of populations at their respective reefs of collection, the observed declines in size at maturity were interpreted either as compensatory responses to per capita increases in resource availability (e.g., food, shelter, or their interaction: see Parrish and Polovina, 1994) at reduced population densities or as behavioral responses among females of different sizes. The response was observed at both Necker bank and Maro Reef, and both areas had been harvested heavily by the fishery prior to that time (Polovina, 1989).

Lobster research in the early 1990s continued to focus on spiny lobster. DeMartini et al. (1993) presented data suggesting that, between pre-exploitation (1978-81) and peak exploitation (1991) periods, size-specific fecundity increased 16% for spiny lobster at Necker bank, where most fishing effort and the majority of catches had occurred, but not at Maro Reef, another area where fishing effort and catch was high prior to 1991 (Fig. 2). If real (and there was no reason either then or now to doubt that specimens were representative), this average 16% increase in the fecundity of individual females at Necker was biologically important as well as statistically significant. Increased

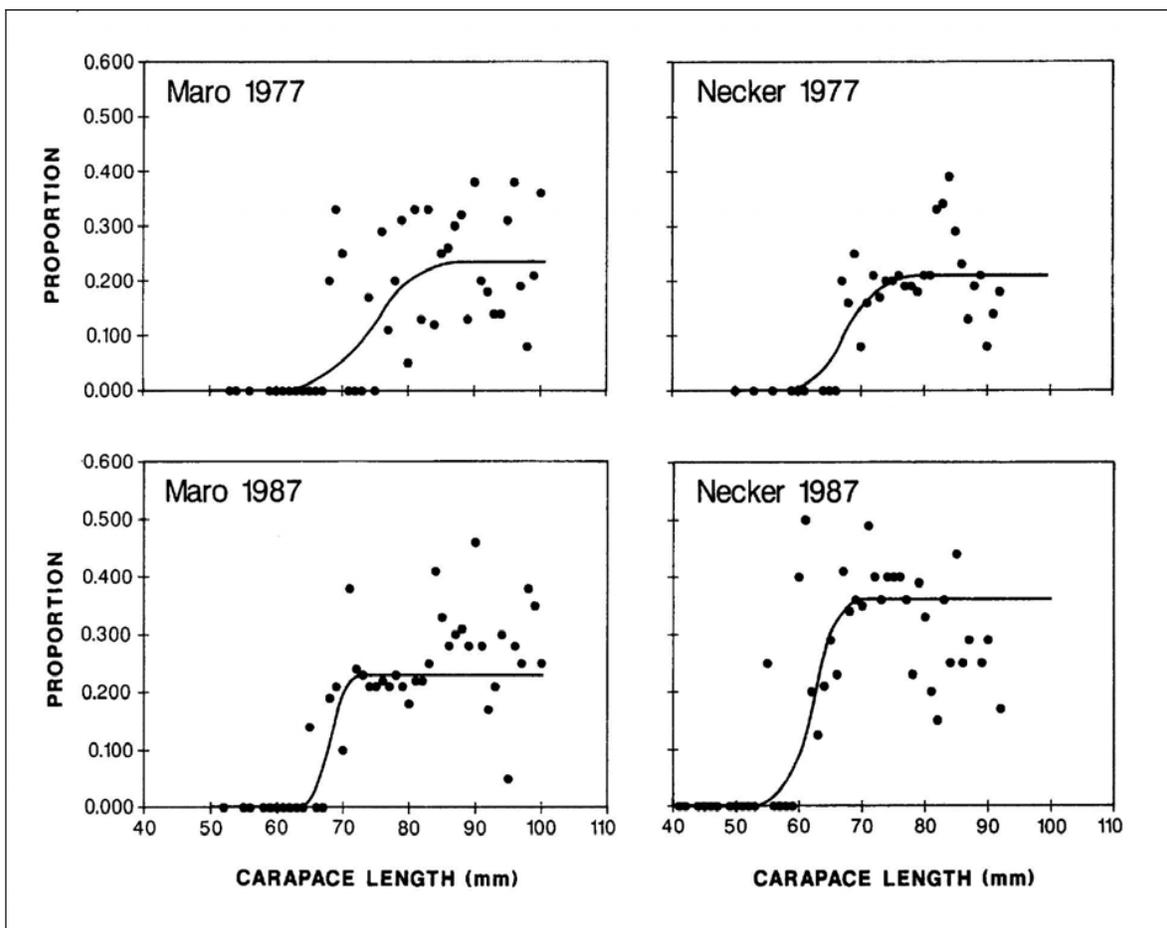


Figure 1. Proportion of female spiny lobsters at Necker bank and Maro Reef with eggs as a function of carapace length for 1977 and 1987. Source: Figure 4 of Polovina (1989).

egg production by individual females was interpreted as consistent with greater per capita resource availability at lower densities at Necker (DeMartini et al., 1993). It is intriguing that this compensatory increase in reproductive effort occurred despite sound evidence for a shift into a lower productivity regime between the two sampling periods (Polovina et al., 1994; Polovina 2005). A preliminary attempt to test the prediction that, at greater per capita food availability, the somatic condition of individual spiny lobster should have increased, produced equivocal results (Parrish and Martinelli-Liedtke, 1999).

Lobster density-fecundity relations were again revisited, adding size-specific fecundity data collected in 1999. An additional 18% increase in size-specific fecundity was observed, for a cumulative one-third increase between the pre-exploitation period and shortly before fishery closure (Fig. 3; DeMartini et al., 2003)—a striking augmentation of per capita egg production. As for the initial fecundity comparisons using 1991-collected specimens (DeMartini et al., 1993), the capture locations of specimens were cloaked to protect against unwitting bias when counting egg samples for fecundity comparisons, further ensuring that the observations were real. Fishery-dependent catch-

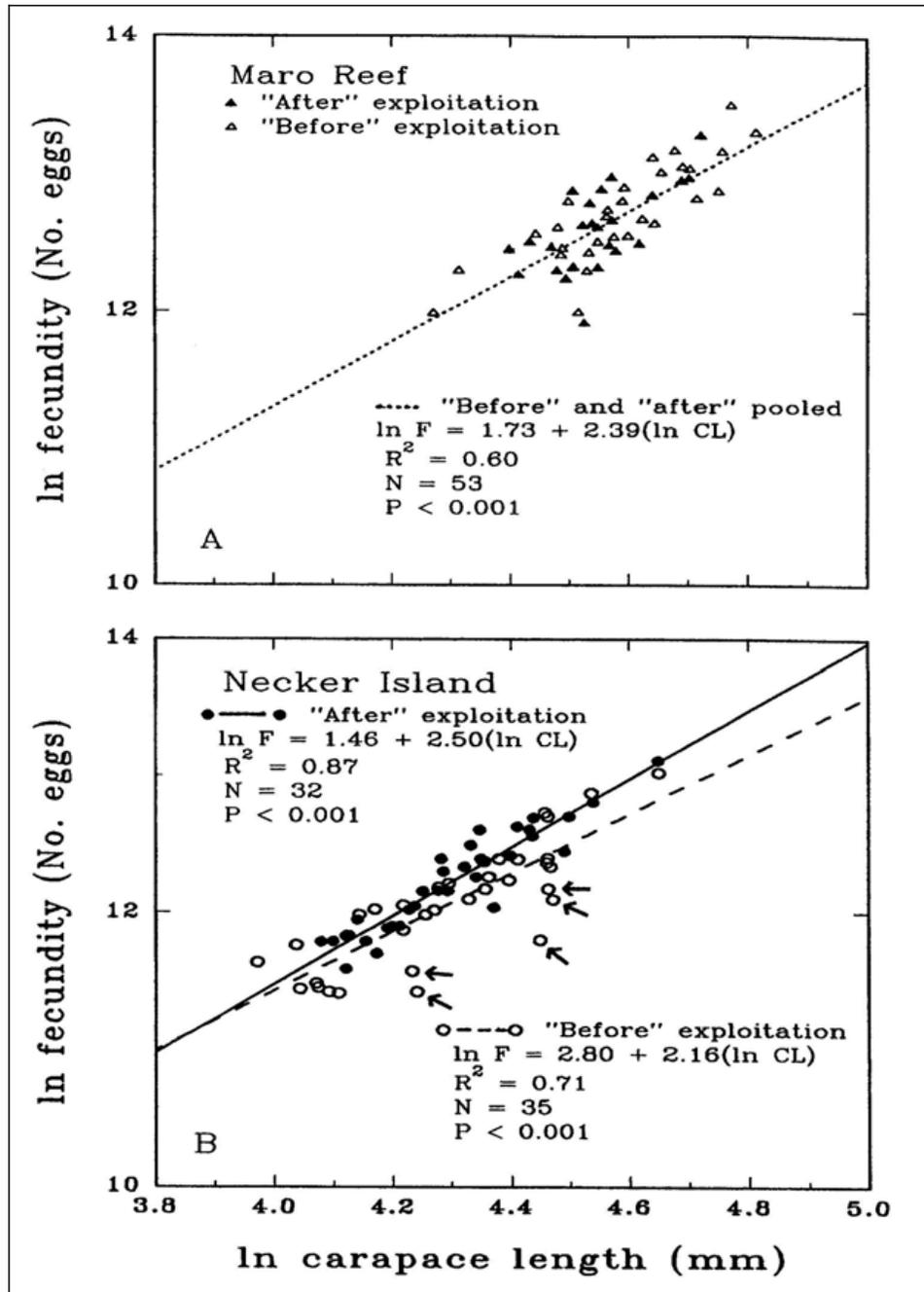


Figure 2. Scatterplots, least squares regressions, and regression statistics for fecundity (ln number of eggs) versus ln carapace length (in mm) for berried female spiny lobster trapped at two locations in the NWHI. Maro Reef (top): Data for the "before" (1978-81) and "after" (1991) periods are pooled for the regression analysis but plotted separately. Necker (bottom): Data for the "before" and "after" periods are plotted and analyzed separately. Arrows indicate the five most extreme "before" data that were deleted in a conservative re-analysis of the data. Source: Figure 1 of DeMartini et al. (1993).

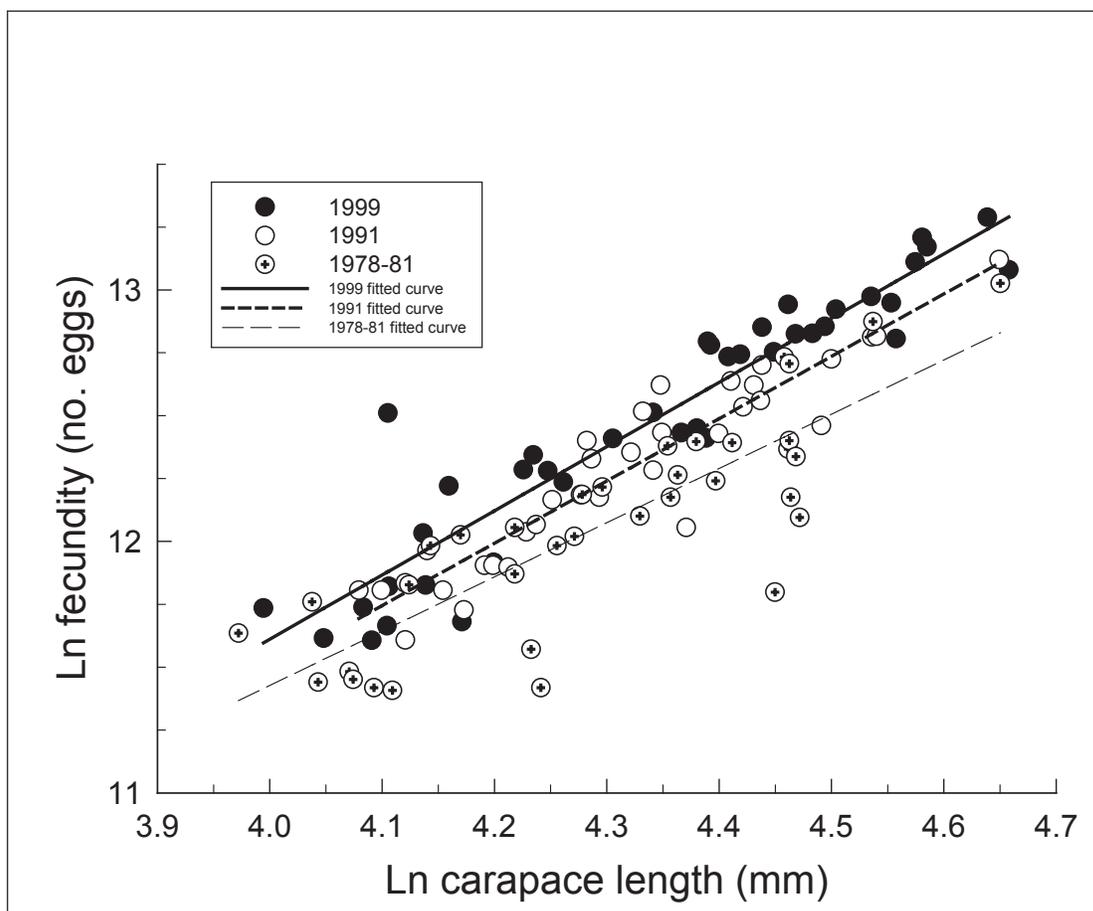


Figure 3. Log-linear scatterplot of fecundity (ln number of brooded eggs) versus carapace length (ln CL, in mm) for spiny lobster collected at Necker bank during three periods (1978-81, 1991, and 1999). Source: Figure 4 of DeMartini et al. (2003).

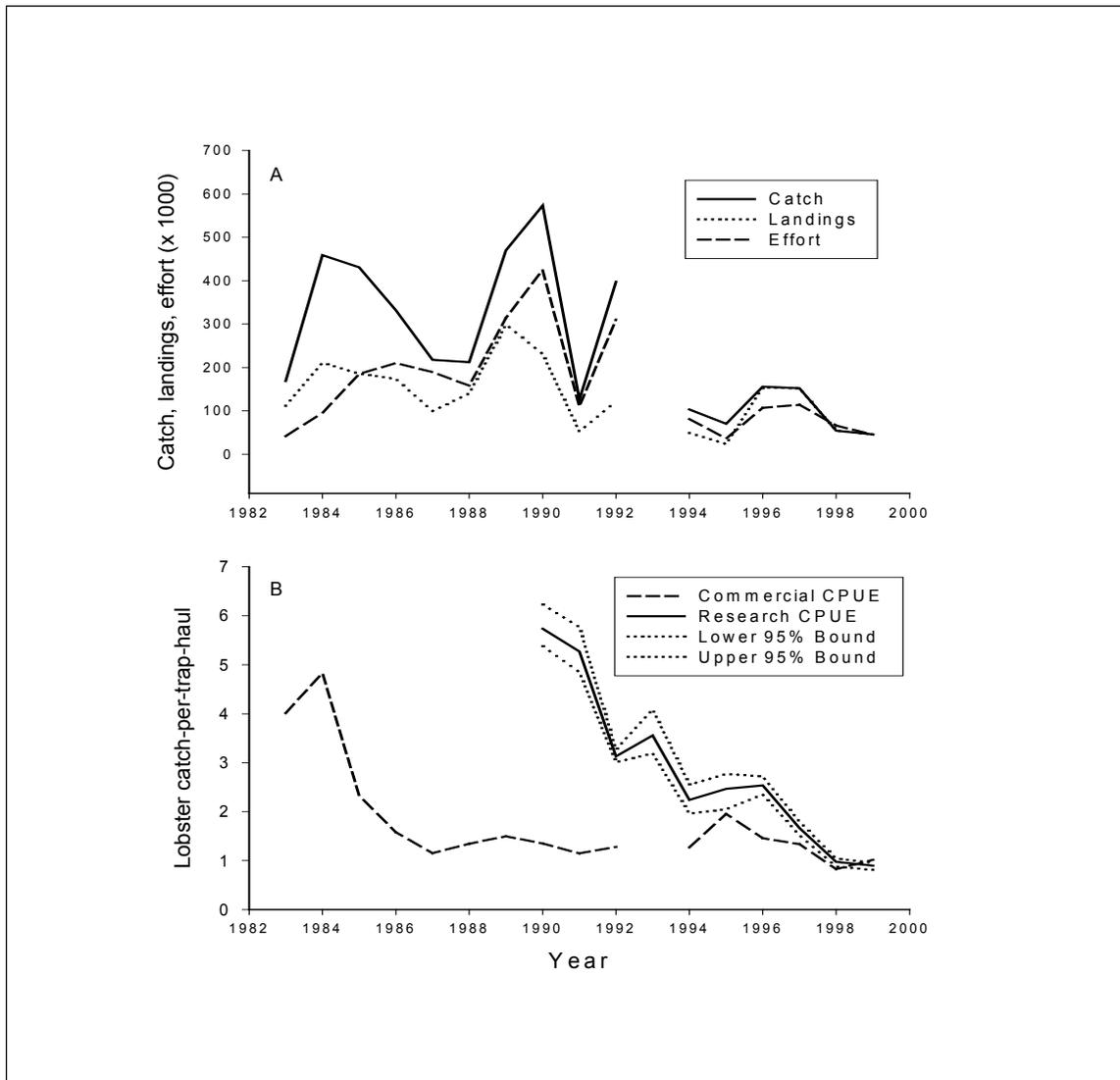


Figure 4. Time series plots of (A) the Necker bank, NWHI commercial trap catch and landings of Hawaiian spiny lobster (no. lobsters x 1000) and effort (no. trap-hauls x 1000); and (B) total spiny lobster catch per-trap-haul (CPUE) at Necker bank during the 1983-99 commercial fishing seasons and as assessed on 1988-99 lobster research cruises. Dashed lines framing the research curve in B represent bootstrapped 95% confidence intervals. Replotted from Figure 1 of DeMartini et al. (2003) to show year-specific estimates.

per-unit-effort (CPUE) data and analogous, fishery-independent data collected on annual lobster research surveys suggested successive half order of magnitude decreases in abundance between the early 1980s-early 1990s and between the early-to-late 1990s, respectively (Fig. 4; DeMartini et al., 2003). Detailed estimates of the mean and variance of fecundity estimates in 1999 further allowed for a characterization of size-specific egg production, which showed that, just before the fishery was closed, nearly one-half of all of spiny lobster eggs at Necker bank were being produced by small individuals of 50-57 mm tail (abdomen) width (DeMartini et al., 2003). The size (mass) of individual eggs, although independent of female body size, increased by an estimated 11% for spiny lobster at Necker bank between 1991 and 1999, a response further consistent with greater per capita food availability at lower densities (DeMartini et al., 2003).

At the same time, additional declines in size at maturity of female spinys were occurring during the early 1990s (Fig. 5A; DeMartini et al., 2002). This study also provided the first formal estimates of size at sexual maturity for female slipper lobster in the NWHI (Fig. 5B; DeMartini et al., 2002). The authors noted a problem of unacceptably poor precision when using conventional external characteristics (berried condition) to macroscopically score the maturity of individual slipper lobster. A companion paper (DeMartini and Williams, 2001) provided size-specific fecundity (Fig. 6) and egg size estimates for slipper lobster at Maro Reef, where this species was then targeted by the fishery.

In response to the precision problem encountered when evaluating maturity of slipper lobster, a morphological metric was developed for identifying body size at functional maturity; and this was verified by histology to closely approximate physiological maturity (DeMartini et al., 2005). This metric (an allometric pleopod-to-tail width relation) was derived for spinys, as well as slippers, although its primary application was for the latter (Fig. 7; DeMartini et al., 2005). Size at maturity of slipper lobster is now estimable from data collected on one or two annual research cruises—a capability previously lacking for this species. Prior to this, estimates based on berried condition (then the only gross characteristic available) were highly imprecise as well as inaccurate (biased), even if data were pooled over many years (Fig. 5B; DeMartini et al., 2005).

DATA NEEDS, MANAGEMENT IMPLICATIONS, AND FUTURE RESEARCH

Current estimates of size-specific, annual egg production for lobster individuals and populations are limited by lack of information on the spawning frequency of individual females and how this might vary among females of different sizes (DeMartini et al., 2003). Long-term characterizations of size-specific spawning seasonality are necessary for both spinys and slippers. Much, perhaps all, of the data required on seasonal estimates of berried condition are being collected as part of an ongoing, large-scale tag-recapture program (see below).

More information is necessary on the scope of compensatory responses for which NWHI lobster are capable. Additional comparisons of size-specific fecundity and size at sexual maturity would require the sacrifice of relatively few (at most several hundred) specimens. Such an evaluation would provide much discriminatory power to test the

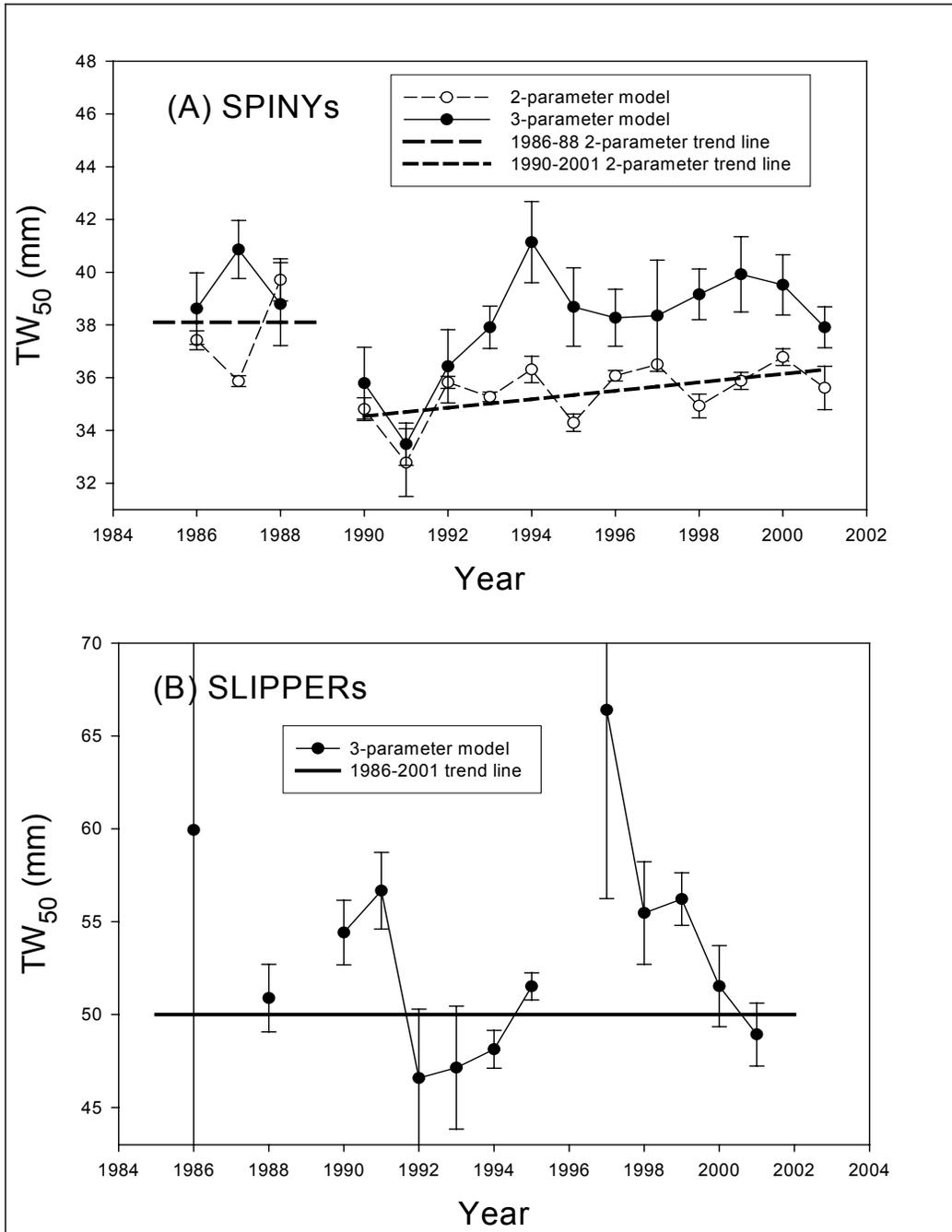


Figure 5. Scatterplot and fitted trend line for survey-year estimates of tail width at which 50% of all females were sexually mature (TW_{50}) during the period from 1986 to 2001, for (A) Hawaiian spiny lobster and (B) slipper lobster. Vertical lines indicate ± 1 SE of the TW_{50} estimate for the specific survey-year. Bold lines indicate means of (spiny, 1986-88; slipper, 1986-2001) or trends in (spiny, 1990-2001) TW_{50} estimates. Source: Figure 2 of DeMartini et al. (2002).

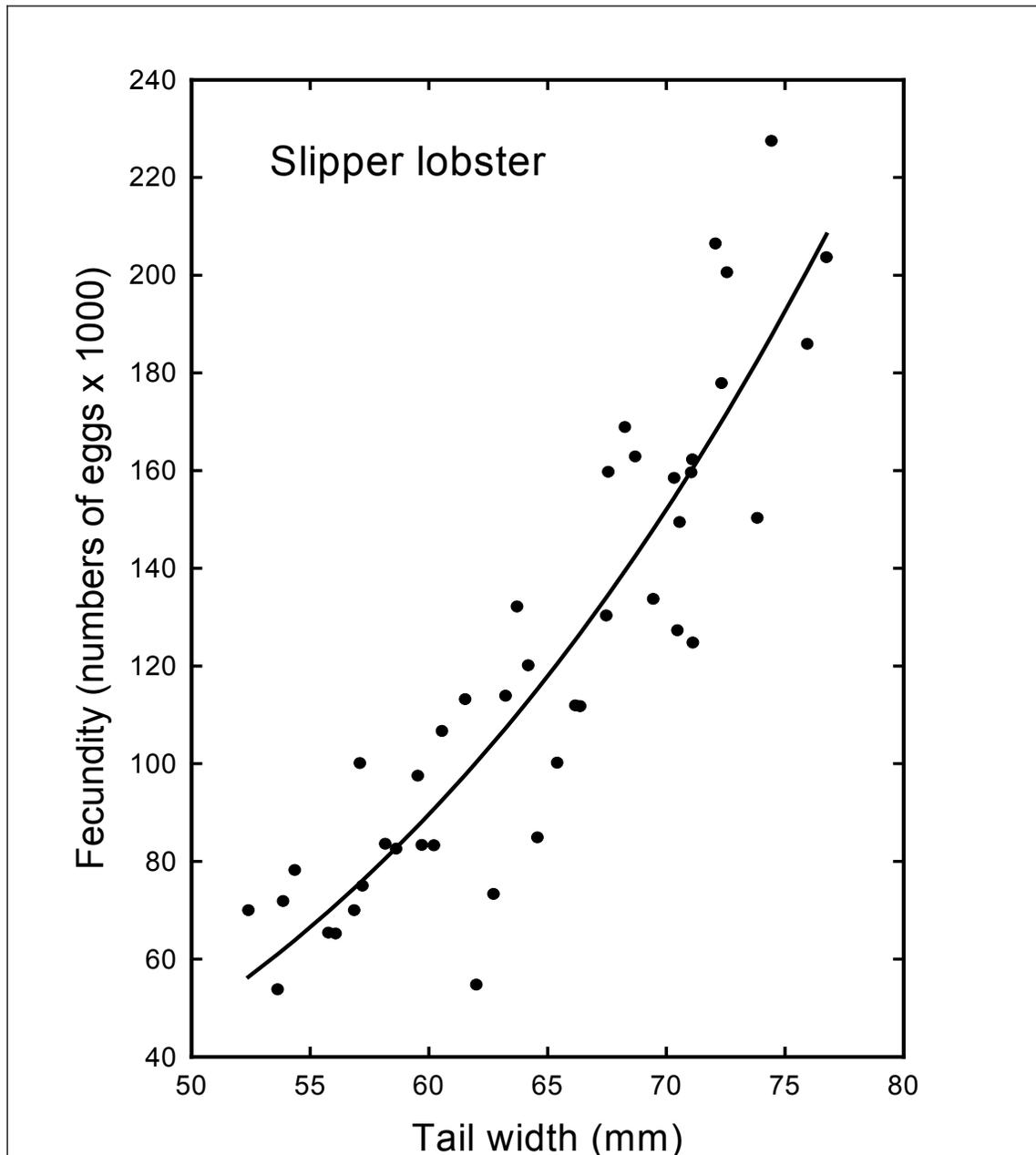


Figure 6. Scatterplots and best fit (nonlinear) relationship between fecundity (F, the number of eggs present on pleopods) and tail (abdomen) width (TW, mm) of slipper lobster from Maro Reef, NWHI, in June 1999. Source: Figure. 1 of DeMartini and Williams (2001).

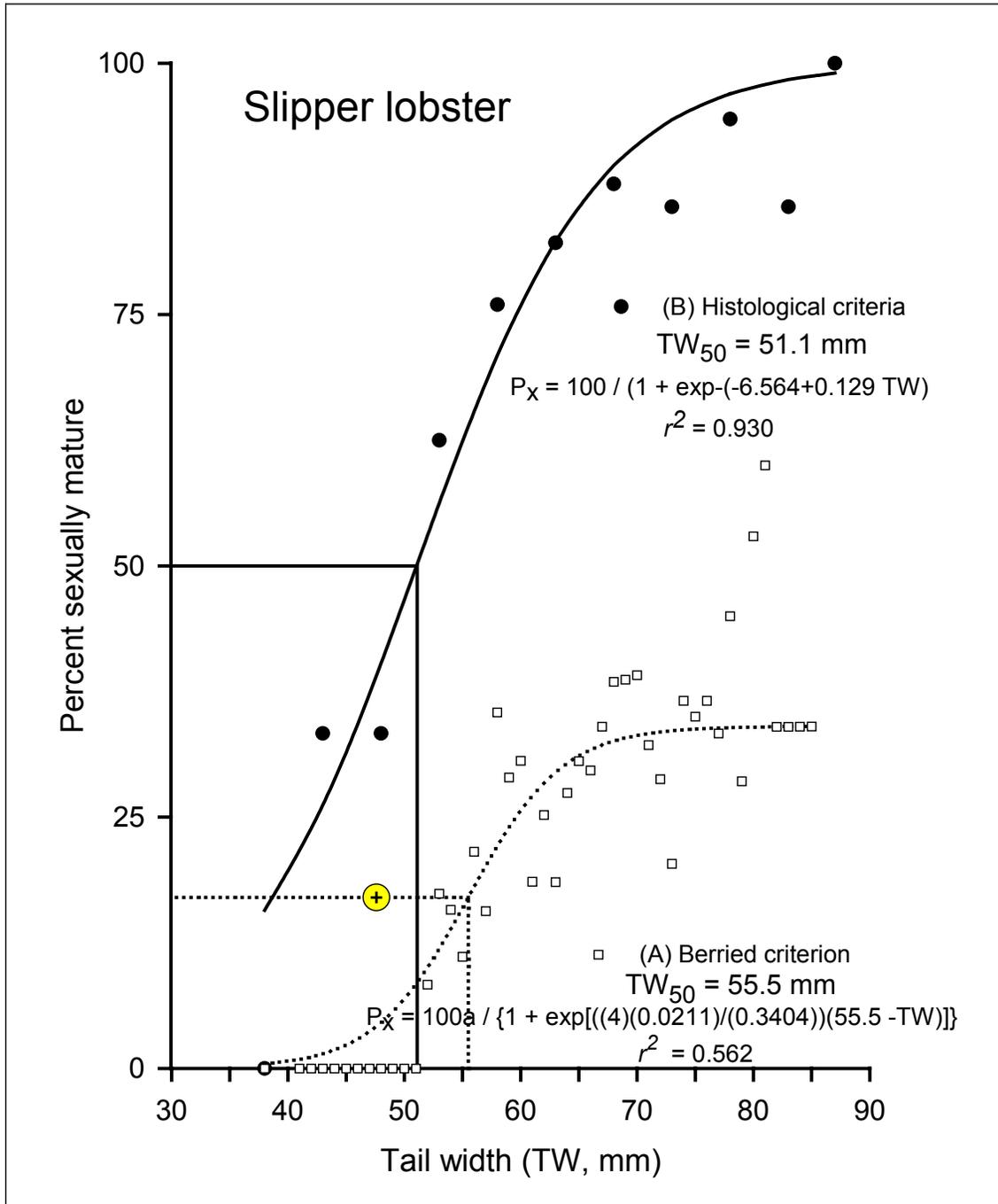


Figure 7. Scatterplots and fitted curves of the relations between body size (tail width, TW) and percent sexual maturity based on (A) functional maturity gauged by presence-absence of berried condition; overlaid on (B) gonadal maturation gauged by microscopic examination of ovaries, with the pleopod length-based morphometric maturation point estimate of size at functional maturity indicated by the large circle with cross-hairs, for slipper lobster. A 3-parameter logistic equation was necessary to fit curve A; a 2-parameter logistic was sufficient to fit curve B. Source: Figure 4 of DeMartini et al. (2005).

opposite predictions that size-specific fecundity should decrease while size at maturity increases at higher population densities. One necessary precaution is that a minimum one-year lag between a density rebound and collection would be required, and specimens would have to be collected before a fishery were to re-open and reduce densities.

It is further obvious that complementary research on growth, mortality, and movement is needed before a complete suite of vital rate estimates enable spatially-structured stock assessments for spiny and slipper lobsters in the NWHI. Obtaining estimates of individual growth rates is problematic because of the continuing dearth of information on age and growth of lobsters in the NWHI. A continuing, long-term tag-recapture study, utilizing both external and PIT tags is building the capacity to estimate movement patterns, rates of natural mortality and growth, and fishing mortality rates (if a fishery were to be re-opened: G. DiNardo, National Oceanic and Atmospheric Administration (NOAA) Fisheries, Pacific Islands Fisheries Science Center, Honolulu, pers. comm.).

Methods for aging lobsters are seriously complicated by the lack of an available age-marker that can be used to characterize the growth of individuals. Lobsters, like other crustaceans that molt, provide no evidence of sizes at previous ages such as growth checks recorded in a persistent hard part, so in most cases growth can be described only from observations of tag-recaptured individuals (longitudinal study). If the latter approach is taken, correction for possible growth retardation due to capture, handling, and the tag itself may need to be evaluated. Recent characterizations of the age and retrospective growth of individual crustaceans using chemical or morphological assays of the autofluorescent age-pigment lipofuscin have been encouraging (Ju et al., 2003; Sheehy et al., 1999), although some complications in distinguishing chronological from physiological age still persist.

One partial solution to the problem of aging lobsters and other crustaceans, regardless of whether the approach is longitudinal or retrospective using conventional methods, involves effectively decoupling the growth increment per molt from molting frequency for lobster spanning the range of sizes and ages in the population. One type of “biological tag” (a tissue implant that records molting history) has recently been shown capable of adequately estimating molt frequency for several spiny lobster species elsewhere (Melville-Smith et al., 1997), thereby providing the precise estimates of size-specific growth per molt needed for stage-structured stock assessment.

A preliminary series of tank experiments evaluating whether telson tissue implants could be used to characterize molting frequency were encouraging for slipper lobster but completely unsuccessful for spinys. These experiments, conducted by personnel at the Kewalo Research Facility, Honolulu Laboratory, NOAA Fisheries, in 2000, were compromised because spiny lobster experienced developmental problems during molting that were likely related to unnaturally high water temperatures or other aspects of water quality. Carefully executed experiments conducted in a temperature-controlled environment with improved water quality would be required; the precise estimates of size-specific molting frequency that might result from such an effort would have sufficient importance to warrant the expense.

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