BioOne COMPLETE

Spatial and Temporal Variability in Growth of Hawaiian Spiny Lobsters in the Northwestern Hawaiian Islands

Author: O'Malley, Joseph M.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 2009(2009) : 325-342

Published By: American Fisheries Society

URL: https://doi.org/10.1577/C09-031.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 1:325–342, 2009
© Copyright by the American Fisheries Society 2009
DOI: 10.1577/C09-031.1

[Article]

Spatial and Temporal Variability in Growth of Hawaiian Spiny Lobsters in the Northwestern Hawaiian Islands

JOSEPH M. O'MALLEY*

Hawaii Institute of Marine Biology, University of Hawaii, Post Office Box 1346, Kaneohe, Hawaii 96744, USA

Abstract.—Growth rates were estimated for recaptured Hawaiian spiny lobsters *Panulirus marginatus* tagged between 2002 and 2007 at Necker Island (23°30′N; 164°35′W), Gardner Pinnacles (25°00′N; 168°50′W), and Maro Reef (25°30′N; 170°45′W) in the Northwestern Hawaiian Islands (NWHI). The location and year-specific nature of the tag–recapture cruises enabled investigation of spatial and temporal variability in growth. Mean growth rates, estimated by using the von Bertalanffy and Schnute growth models and fitted via a maximum likelihood technique, differed between sexes and particularly among locations and years. Male lobster growth rates at Necker Island were, in general, one-third those at Gardner Pinnacles and one-half those at Maro Reef. Female lobsters exhibited the same pattern with less-pronounced differences. Maro Reef lobsters exhibited several abrupt, significant growth reductions among years, while Necker Island lobster growth rates increased significantly from 2004 to 2005. Model results also indicated substantial individual variability in growth. Neither density nor temperature could account for the differences in growth rates. No palinurid species studied to date has shown such spatial variability in growth, and only one panilurid species has exhibited similar variability on a temporal scale. Recognition of and accounting for the mean and individual variability in a life history trait of this endemic species will result in more accurate stock assessments and, ultimately, a better understanding of lobster dynamics and the NWHI coral reef ecosystem.

Sustainable exploitation of commercially valuable species requires accurate estimates of somatic growth and an in-depth understanding of the causes of any spatiotemporal variability associated with those estimates. Growth rates are important components of yield equations (Beverton and Holt 1957) and are also used in other methods to assess stocks, including mortality (Griffiths and Harrod 2007), maturity schedules (Clark et al. 1999), recruitment or settlement (Wahle et al. 2004), spawner–recruit relationships (Sheehy 2001), and fishing selectivity (Jeffery and Taggart 2000). Failing to account for growth variability in population models introduces biases to biomass estimates, which in turn can lead to inappropriate management schemes and exploitation levels. This may be especially true of palinurid lobsters because many species exhibit spatial and temporal growth variability associated with density (Pollock 1991; McGarvey et al. 1999), environmental conditions (Chittleborough 1975; Pollock and Shannon 1987; Pollock et al. 1997), and food availability (Newman and Pollock 1974; Edgar 1990).

The Hawaiian Archipelago consists of the main Hawaiian Islands (Hawaii to Niihau) and the Northwestern Hawaiian Islands (NWHI), a series of islands, reefs, seamounts, and atolls (hereafter referred to as banks) extending approximately 2,000 km across the subtropical Pacific (Figure 1). The Hawaiian spiny lobster *Panulirus marginatus* is endemic to the Hawaiian Archipelago and Johnston Atoll. Pre-exploitation surveys (1976–1978) indicated that the average Hawaiian spiny lobster size increased in a northwesterly direction along the NWHI (Uchida et al. 1980). In particular, Necker Island, located near the southeastern end of the NWHI, had the smallest Hawaiian spiny lobsters but also the greatest abundance (Uchida et al. 1980).

A commercial fishery targeting Hawaiian spiny lobsters in the NWHI began in the mid-1970s. Fishing effort remained relatively low until 1984, when the introduction of new traps resulted in a threefold increase in effort in just 2 years. Despite near-annual stock assessments from 1985 to 2000, the NWHI lobster fishery suffered severe declines in catch per unit effort (CPUE; Figure 2) and was closed in 2000 because of increasing uncertainty in the population models used to assess stock status. The uncertainty stems from the assumption of synchronous dynamics, regardless of location and time period, among bank-specific lobster populations (Botsford et al. 2002). For example, previous Hawaiian spiny lobster tagging studies at the NWHI (Kure Atoll in 1979–1983 and French Frigate Shoals in 1981–1983) used Fabens' (1965) method to estimate the conventional von Bertalanffy growth parameters: asymptotic maximum length (L_∞) and growth constant (K; MacDonald 1984).

Subject editor: Patrick Sullivan, Cornell University, Ithaca, New York

* E-mail: joseph.omalley@noaa.gov

Received June 23, 2009; accepted September 11, 2009
Published online December 21, 2009

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

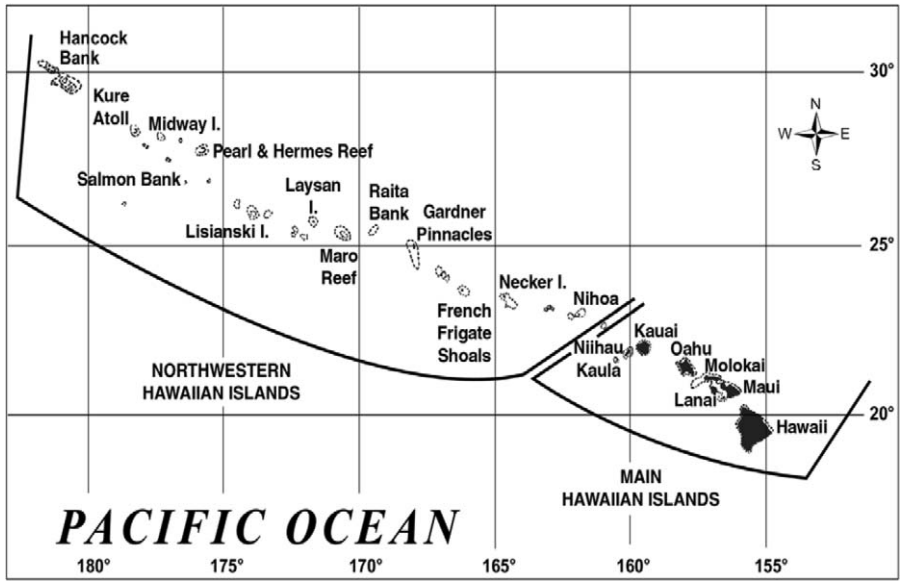


FIGURE 1.—Map of the Hawaiian Archipelago, including the Northwestern Hawaiian Islands.

The growth estimates (male $K = 0.27$, female $K = 0.35$) were used in a Beverton–Holt yield equation to estimate Hawaiian spiny lobster abundance at all banks in the NWHI (Polovina 1985). Growth estimates were also derived from modal progression analysis of size frequencies of Hawaiian spiny lobsters captured during research cruises at Necker Island in 1986–1988 (growth rate values were unreported; Polovina and Moffitt 1989) and were used to determine size at recruitment to the fishery and age-specific CPUE in the 1989–1993 assessments. The use of these growth rates in NWHI-wide assessments ignored any spatial and temporal variability that might be associated with those values.

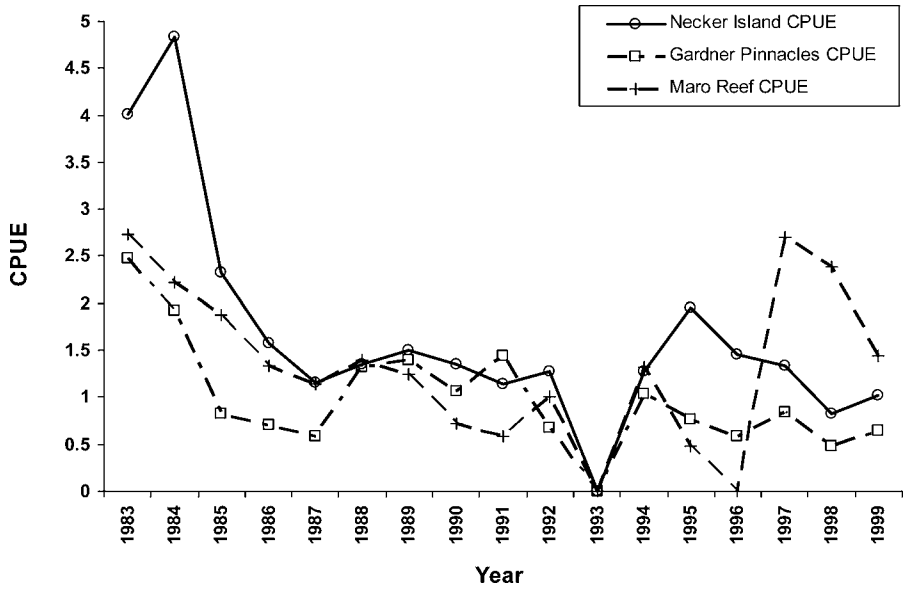


FIGURE 2.—Commercial catch per unit effort (CPUE; number of lobsters captured per trap haul) for Hawaiian spiny lobsters at Necker Island, Gardner Pinnacles, and Maro Reef, Northwestern Hawaiian Islands, from 1983 to 1999. The fishery was temporarily closed in 1993.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Acknowledging and discounting the assumption of synchronous dynamics represented a change in NHWI Hawaiian spiny lobster population dynamics theory from a single archipelago-wide population to a series of discrete metapopulations separated by the deep water between banks and connected only by larval dispersal. To examine bank-specific lobster dynamics, an extensive tagging program was conducted from 2002 to 2008. A preliminary examination of the 2002–2003 Necker Island tagging data indicated that a metapopulation approach is appropriate because the estimated Hawaiian spiny lobster growth differed significantly from that observed at Kure Atoll and French Frigate Shoals from 1979 to 1983 (O'Malley and MacDonald 2009).

The objective of this study is to investigate NWHI Hawaiian spiny lobster metapopulation dynamics by describing location-specific (Necker Island, Gardner Pinnacles, and Maro Reef) and year-specific (2002–2008) growth rates. Also examined are the effects of density and temperature, two common drivers of growth variability.

Methods

Tag–recapture data.—Hawaiian spiny lobster tagging was conducted aboard chartered commercial fishing vessels at the banks where the NWHI commercial fishery was primarily concentrated: Necker Island (23°30′N; 164°35′W); Gardner Pinnacles (25°00′N; 168°50′W); and Maro Reef (25°30′N; 170°45′W; Figure 1). Trapping took place within the entirety of each bank, although effort was concentrated in areas with greater densities of Hawaiian spiny lobsters, as indicated by habitat (depth and sand versus hard bottom) and the captain's previous lobster fishing experiences in the NWHI. Tagging began at Necker Island in 2002, expanded to Maro Reef in 2004, and then extended to Gardner Pinnacles in 2006; tagging took place at all three banks in 2006–2008. The annual tag–recapture cruises occurred between June and September of each year.

Hawaiian spiny lobsters were captured by using standard commercial molded black polyethylene Fathoms Plus (San Diego, California) traps, which are dome-shaped and single-chambered, with two entrance cones (dimensions = 980 × 770 × 295 mm, inside mesh dimensions = 45 × 45 mm). Mesh paneling was placed over the escape vents to prevent the release of small lobsters, thereby maximizing the size range of captured lobsters. Fifteen strings consisting of 20 traps/string were soaked overnight; each trap was baited with 1 kg of Pacific chub mackerel *Scomber japonicus*. Initially (i.e., at Necker Island in 2002), Hawaiian spiny lobsters were tagged by using polyethylene streamer tags (Hallprint, Inc., Victor Harbor, South Australia) inserted through the abdominal flexor muscle at the juncture of the cephalothorax and abdomen. However, research indicated that these tags were not suitable for Hawaiian spiny lobsters because of excessive tag loss (O'Malley 2008). All subsequent tagging was done by using passive integrated transponder (PIT) tags (Destron Technologies, South St. Paul, Minnesota) injected into the distal tail segment (O'Malley 2008). The PIT tags were detected with a Destron Technologies Model 2001F-ISO portable transceiver (Digital Angel Corporation, St. Paul, Minnesota). For each tagged and recaptured lobster, the PIT tag number, carapace length (CL; nearest 0.01 mm), sex, date of capture, and position of release (latitude and longitude determined using a Global Positioning System unit) were recorded. All lobsters were released on the seafloor in the immediate area of recapture via a release cage (O'Malley 2008). Each tag–recapture cruise had at least one tagger from previous cruises, which provided continuity in the tagging process. An important detail of this work is that because the commercial fishery was closed and because poaching and recreational fishing are highly unlikely given the remoteness and regular monitoring of the NWHI, tagged lobsters were recaptured by researchers during the annual tag–recapture cruises only.

Growth analysis.—Hawaiian spiny lobster recapture data were first aggregated on a bank-specific level to examine spatial (among-bank) differences in growth rates (Necker Island, 2002–2008; Gardner Pinnacles, 2006–2008; and Maro Reef, 2004–2008). In these data sets, if individuals were recaptured more than once, only the initial and final capture information was used in the analysis and no immediate recaptures (i.e., lobsters captured during the same tagging cruise) were included. This was done to ensure equal weight in the analysis of any individual's specific growth rate and to maximize the time at liberty. To estimate annual growth and to examine temporal variability, recapture data were partitioned into year-specific data sets within each bank.

Bank-, year-, and sex-specific data were fitted to the von Bertalanffy and Schnute growth models with Francis' (1988a, 1995) maximum likelihood method by using the GROTAG program designed by Simpfendorfer (2000) for the Microsoft Excel solver function (Microsoft Excel version 2002; Microsoft Corp., Redmond, Washington). Both models estimate growth by using the parameters g_{α} and g_{β}, which represent mean annual growth increments (mm/year) of chosen reference lengths α and β (Francis 1988a, 1995). Growth rates at these specific sizes are directly

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

observable and are therefore biologically meaningful. In the case of the von Bertalanffy growth model, these parameters have better statistical properties than K and L_∞, particularly when the entire size range of the species is not represented in the data (Sainsbury 1980; Francis 1988a, 1988b; Haddon 2001). Hawaiian spiny lobster reference lengths α and β for both models were chosen so that within each data set, the values were well represented while maintaining the majority of individuals between the two values (Francis 1988a). This allowed direct spatial and temporal comparisons within the sexes. The male α and β were set at 75 and 110 mm CL, respectively, whereas the female α and β were set at 70 and 100 mm CL, respectively.

The von Bertalanffy growth model was applied by using Francis' (1988a) reparameterization of Fabens' (1965) growth model for tagging data. Following Francis (1988a), the expected length increment (ΔL) for a Hawaiian spiny lobster tagged at length L_1 and at liberty for time ΔT is given by:

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T}\right]. \quad (1)$$

To compare Hawaiian spiny lobster growth rates with other palinurid growth estimates, model outputs were converted to the von Bertalanffy growth parameters K and L_∞ following Francis (1988a):

$$K = \log_e[1 + (g_\alpha - g_\beta)/(\alpha - \beta)] \quad (2)$$

and

$$L_\infty = (\beta g_\alpha - \alpha g_\beta)/(g_\alpha - g_\beta). \quad (3)$$

Differences in the set reference values of α and β for males and females prevented direct comparison of growth between the sexes; therefore, female lobster g_{75} and g_{110} were estimated by using (Francis 1988a):

$$g_\gamma = [(\gamma - \alpha)g_\beta + (\beta - \gamma)g_\alpha]/(\beta - \alpha). \quad (4)$$

Francis (1995) also created a mark–recapture "equivalent" of Schnute's (1981) size-at-age model by using the same parameters (α, β, g_α, and g_β) to describe growth. Following Francis (1995: equation 5.1), the ΔL for a Hawaiian spiny lobster tagged at length L_1 and at liberty for ΔT is given by:

$$\Delta L = -L_1 + [L_1^b e^{-a\Delta T} + c(1 - e^{-a\Delta T})]^{1/b}, \quad (5)$$

where

$$a = \log_e\left(\frac{\beta^b - \alpha^b}{\lambda_\beta^b - \lambda_\alpha^b}\right) \quad \text{if } b \neq 0, \quad (6)$$

$$c = \frac{\beta^b \lambda_\alpha^b - \alpha^b \lambda_\beta^b}{\lambda_a^b - \alpha^b + \beta^b - \lambda_\beta^b} \quad \text{if } b \neq 0, \quad (7)$$

$$\lambda_\alpha = \alpha + g_\alpha, \quad (8)$$

and

$$\lambda_\beta = \beta + g_\beta. \quad (9)$$

Parameter b, which is analogous to the parameter b in Schnute's (1981) model, has no biological meaning and is generally thought of as describing curvature in the model.

Both growth models were fit by using the negative log-likelihood function (Francis 1988a):

$$\lambda = \sum_i \log[(1 - p)\lambda_i + p/R], \quad (10)$$

where

$$\lambda_i = \exp\frac{-1/2(\Delta L_i - \mu_i - m)^2/(\sigma_i^2 + s^2)}{[2\pi(\sigma_i^2 + s^2)]^{1/2}}, \quad (11)$$

R = the range of observed growth increments, μ = the expected growth increment, m = the mean measurement error, s = standard deviation of measurement error, and σ = the standard deviation of the growth variability. Also estimated were the coefficient of variation of growth variability (v) and outlier contamination (p). To describe growth variability, σ was related to μ ($\sigma_i = v\mu_i$) by assuming an increase in growth variability as the size of the growth increment increases (Francis 1988a).

The GROTAG methodology cannot accurately determine m and s and cannot distinguish between variability in growth and measurement error because individuals with very short times at liberty were removed from the analysis. Therefore, m and s were fixed based on independent values estimated from differences in length at release and length at recapture for Hawaiian spiny lobsters that were recaptured within 2 d of tagging (n = 206). The mean and standard deviation of these differences represent an exact measure of measurement error, assuming that no growth occurred between tagging and recapture. It is likely that researchers would detect a Hawaiian spiny lobster that molted within this time period (clean carapace, soft shell). The estimated mean and standard deviation of the differences in size were 0.13 and 0.12 mm, respectively, for males and were 0.16 and 0.17 mm, respectively, for females.

For each data set (bank, years at liberty, sex), the first model was the simplest, fitted with only g_α, g_β, s, and in the case of Schnute model, b. Each subsequent model introduced an additional parameter. Likelihood

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1.—Tag–recapture data for Hawaiian spiny lobsters used in growth analysis by bank and years at liberty (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef; *n* = sample size; DAL = days at liberty).

Bank	Year tagged–year recaptured	*n* tagged	*n* recaptured	DAL Mean	DAL SD
NI	2002–2003	13,944	472	360	11
	2003–2004	11,917	901	364	8
	2004–2005	5,990	629	318	1
	2005–2006	5,177	104	334	8
	2006–2007	1,605	165	373	1
	2007–2008	1,361	85	426	1
	2002–2008	39,994	3,158	609	359
GP	2006–2007	673	43	373	1
	2007–2008	1,146	37	429	4
	2006–2008	1,819	90	501	178
MR	2004–2005	1,911	80	316	4
	2005–2006	2,792	39	374	6
	2006–2007	1,663	105	370	2
	2007–2008	2,648	123	377	4
	2004–2008	9,014	415	503	243

ratio tests were used to determine the final model, where for a significant ($P < 0.05$) improvement in fit, the likelihood value must increase by at least 1.92 with the introduction of one parameter and by at least 3.0 with the introduction of two parameters (Francis 1988a). The 95% confidence intervals (CIs) were estimated by using a bootstrapping method as implemented in GROTAG (Simpfendorfer 2000). Significant differences between data sets were identified by comparing 95% CIs and the extent of bootstrap overlap (Welsford and Lyle 2005). Comparison of CIs has been shown to be a conservative yet effective measure of significance (Schenker and Gentleman 2001).

The von Bertalanffy and Schnute growth models were evaluated by using the second-order bias-corrected Akaike's information criterion (AIC_c). For each data set, the model with the lowest AIC_c value was considered the model that provided the best fit to the data.

To examine the effects of density on Hawaiian spiny lobster growth, individual annual growth rates were regressed on CPUE (i.e., lobsters captured per hauled trap) at Necker Island and Maro Reef, the banks with the longest time series of tag–recapture data. Trap CPUE has been shown to be an adequate proxy for density (MacDonald and Stimson 1980; Polovina 1989); therefore, string-specific trap CPUE (lobsters caught in the same string per hauled trap) was calculated for each recaptured Hawaiian spiny lobster at Necker Island (2002–2003 to 2007–2008) and Maro Reef (2004–2005 to 2007–2008). The regression included release size to account for the effect of size on growth:

$$\begin{aligned}\Delta CL/\Delta t = {} & B_0 + B_1(\text{release size}) \\ & + B_2(\text{string-specific trap CPUE}) \\ & + [B_1(\text{release size}) \\ & \times B_2(\text{string-specific trap CPUE})] \\ & + \varepsilon, \end{aligned} \quad (12)$$

where ε is the error term.

To test the influence of temperature on Hawaiian spiny lobster growth, the 2004–2005 to 2007–2008 Necker Island and Maro Reef estimated growth rates (g_α, g_β) were regressed on sea surface temperature (SST) data. The SST data, collected from the Geostationary Operational Environmental Satellite, were acquired from the National Oceanic and Atmospheric Administration's Oceanwatch Central Pacific website (http://oceanwatch.pifsc.noaa.gov/index.html). The annual mean SST at a given bank and period was calculated by using the start date of the tagging cruise year and the end date of the following year's cruise. The regression included the additional sources of variation to account for their effects on growth:

$$\begin{aligned}\text{estimated growth rate} = {} & B_0 + B_1(\text{year}) + B_2(\text{bank}) \\ & + B_3(\text{sex}) + B_4(\text{SST}) + \varepsilon. \end{aligned} \quad (13)$$

Results

Tag–Recapture Data

In total, 50,827 Hawaiian spiny lobsters were tagged at Necker Island, Gardner Pinnacles, and Maro Reef

TABLE 2.—Hawaiian spiny lobster catch, effort (number of traps hauled), and catch per unit effort (CPUE; lobsters/trap) during tagging cruises by year and location in the Northwestern Hawaiian Islands.

	Necker Island			Gardner Pinnacles			Maro Reef		
Year	Catch	Effort	CPUE	Catch	Effort	CPUE	Catch	Effort	CPUE
2002	13,950	15,000	0.93	—	—	—	—	—	—
2003	11,917	9,400	1.27	—	—	—	—	—	—
2004	7,019	6,900	1.02	—	—	—	1,911	6,000	0.32
2005	6,619	7,660	0.86	—	—	—	2,888	6,300	0.46
2006	2,049	3,400	0.60	703	3,400	0.21	1,764	2,900	0.61
2007	1,845	3,300	0.56	1,222	3,300	0.37	2,834	3,900	0.73
2008	1,441	1,800	0.80	514	1,800	0.29	1,381	1,800	0.77

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

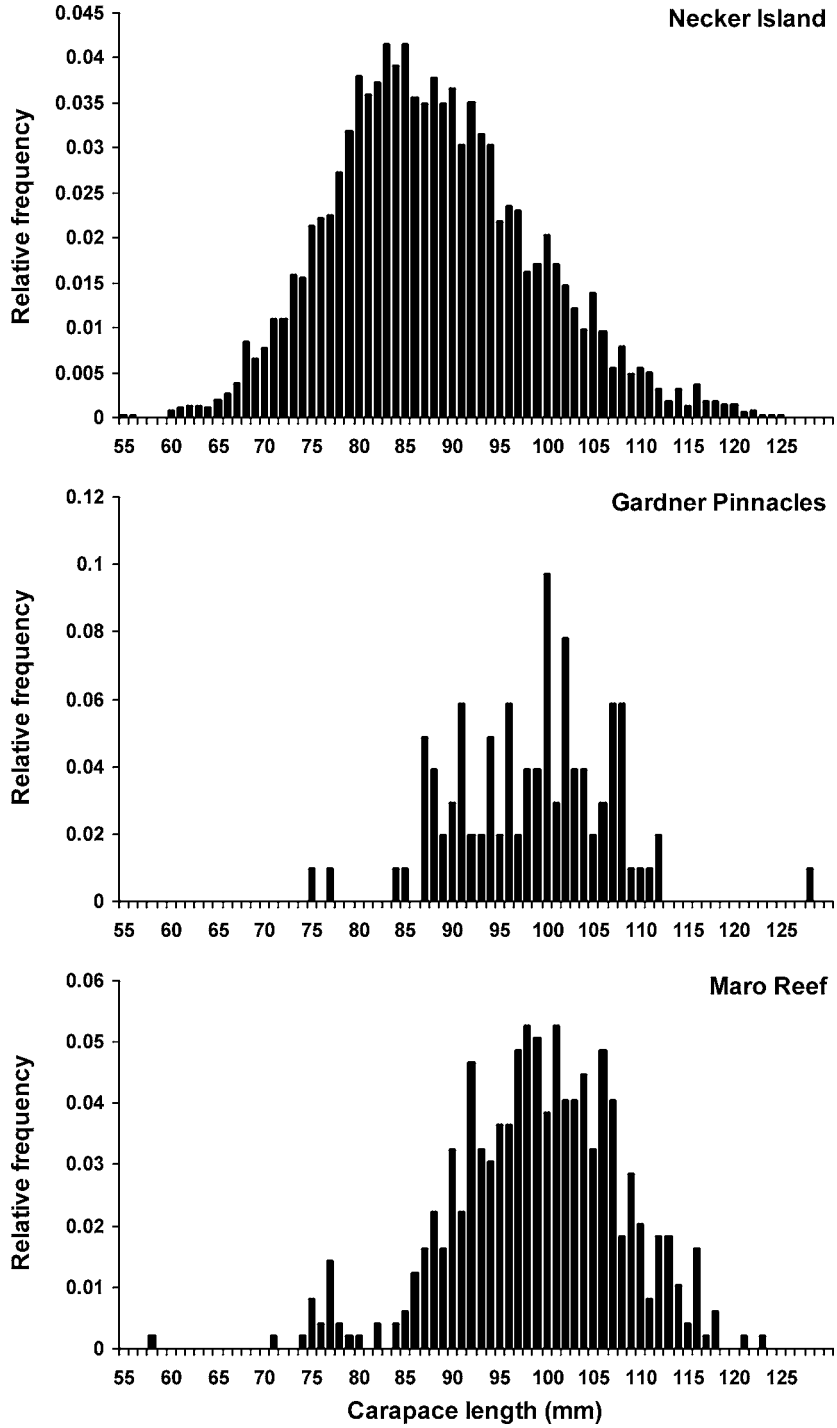


FIGURE 3.—Size-frequency distribution (carapace length, mm) of recaptured Hawaiian spiny lobsters at Necker Island (2003–2008), Gardner Pinnacles (2007 and 2008), and Maro Reef (2005–2008), Northwestern Hawaiian Islands.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 3.—Negative log-likelihood values for differently parameterized von Bertalanffy growth models (Francis 1988a method) used in selection of the optimal model of male and female Hawaiian spiny lobster growth by bank and year (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef; g_α and g_β = mean annual growth increments [mm/year] of chosen reference lengths α and β; s = SD of measurement error; v = coefficient of variation of growth variability; m = mean measurement error; and p = outlier contamination). Values with an asterisk indicate final model selected. Male s and m were fixed at 0.12 and 0.13, respectively; female s and m were fixed at 0.17 and 0.16, respectively.

		Model							
		g_α, g_β, s		g_α, g_β, s, v		g_α, g_β, s, v, m		g_α, g_β, s, v, m, p	
Bank	Year tagged–year recaptured	Male	Female	Male	Female	Male	Female	Male	Female
NI	2002–2003	2,155.2	1,580.1	399.2*	310.2*	399.2	309.1	399.2	309.1
	2003–2004	4,211.2	6,645.0	930.2*	516.6*	929.8	516.6	929.8	516.6
	2004–2005	2,444.9	3,042.9	504.2*	574.7*	503.9	574.5	503.9	574.5
	2005–2006	324.2	403.7	77.0*	89.2*	77.1	89.5	77.0	93.7
	2006–2007	469.5	412.3	131.5*	107.0*	131.5	107.1	131.1	107.1
	2007–2008	248.8	781.9	81.8*	61.9*	81.8	61.8	78.9	61.8
	2002–2008	14,009.1	12,871.2	3,457.5*	2,838.2*	3,461.0	2,840.0	3,461.0	2,840.0
GP	2006–2007	129.2	289.7	42.8*	66.3*	42.7	66.1	42.7	66.1
	2007–2008	52.7	310.2	32.6*	52.0*	32.6	52.2	32.6	52.2
	2006–2008	225.2	754.5	93.1*	141.9*	93.1	141.7	93.1	141.7
MR	2004–2005	271.4	177.9	105.9*	80.5*	106.1	80.5	106.1	80.5
	2005–2006	123.9	185.4	50.7*	46.7*	50.7	46.6	50.7	46.6
	2006–2007	340.1	607.5	101.2*	134.5*	101.2	134.6	101.2	133.8
	2007–2008	203.4	665.9	116.2*	136.8*	116.3	136.4	116.2	137.5
	2004–2008	1,777.2	2,699.9	519.6*	586.7*	520.0	587.4	520.0	619.1

between 2002 and 2007 (Table 1). From 2003 to 2008, 5,052 Hawaiian spiny lobsters were recaptured across all banks; of these recaptures, 2,315 occurred during the next tagging cruise (i.e., lobsters were at liberty for approximately 1 year; Table 1). The variability in the numbers tagged reflects changes in trapping effort when tagging was expanded to different banks rather than large changes in abundance, as evident by CPUE (Table 2). The variability in days at liberty was a result of the research cruise scheduling.

Plots of bank-specific size frequency distributions of recaptured Hawaiian spiny lobsters displayed differences in the population size structure among banks (Figure 3). Mean (±SD) carapace sizes of recaptured

TABLE 4.—Negative log-likelihood values for differently parameterized Schnute growth models (Francis 1995 method) used in selection of the optimal model of male and female Hawaiian spiny lobster growth by bank and year (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef; g_α and g_β = mean annual growth increments [mm/year] of chosen reference lengths α and β; s = SD of measurement error; v = coefficient of variation of growth variability; m = mean measurement error; p = outlier contamination; and b = curvature). Values with an asterisk indicate final model selected. Male s and m were fixed at 0.12 and 0.13, respectively; female s and m were fixed at 0.17 and 0.16, respectively.

		Model							
		g_α, g_β, s, b		g_α, g_β, s, v, b		g_α, g_β, s, v, m, b		g_α, g_β, s, v, m, p, b	
Bank	Year tagged–year recaptured	Male	Female	Male	Female	Male	Female	Male	Female
NI	2002–2003	2,151.0	1,578.0	399.2*	300.4*	398.9	299.3	398.7	446.8
	2003–2004	4,996.0	6,354.0	927.8*	515.7*	927.7	515.7	927.7	515.7
	2004–2005	7,025.0	716.4	493.6*	570.1*	493.4	570.2	493.4	570.2
	2005–2006	999.5	1,001.0	76.1*	87.6*	761.1	89.8	76.1	118.4
	2006–2007	1,424.0	981.0	130.4*	106.7*	130.5	106.8	129.8	106.8
	2007–2008	770.1	759.3	80.3*	61.7*	80.2	61.7	78.1	62.9
	2002–2008	44,314.0	12,682.0	3,440.0*	2,827.0*	3,444.0	2,830.0	3,444.0	2,830.0
GP	2006–2007	317.4	857.1	41.4*	65.3*	41.3	65.2	41.3	65.2
	2007–2008	134.2	827.7	31.6*	51.2*	31.6	51.5	31.6	51.5
	2006–2008	533.5	2,003.0	86.3*	141.0*	86.3	141.2	86.5	141.1
MR	2004–2005	703.4	485.9	102.5*	79.9*	102.8	79.9	102.8	79.9
	2005–2006	398.9	529.5	50.6*	46.5*	50.6	46.5	50.6	46.5
	2006–2007	1,019.0	604.0	98.6*	133.8*	98.6	134.2	98.6	133.2
	2007–2008	967.9	1,744.8	109.5*	136.3*	109.5	136.0	109.5	169.8
	2004–2008	1,513.0	5,138.0	495.2*	509.9*	497.2	512.8	497.6	512.3

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

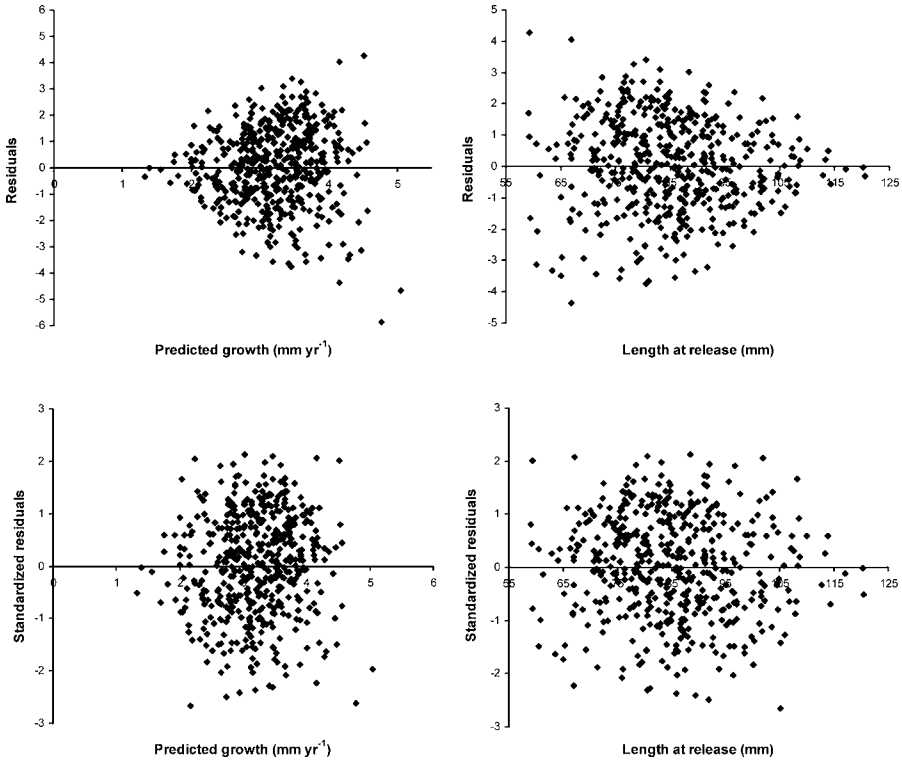


FIGURE 4.—Plots of von Bertalanffy growth model residuals (top panels) and standardized residuals (bottom panels) against predicted growth (left panels; mm carapace length [CL]/year) and length at release (right panels; CL, mm) for male Hawaiian spiny lobsters at Necker Island, Northwestern Hawaiian Islands, 2003–2004.

lobsters were 87.37 ± 10.56 mm CL at Necker Island, 98.93 ± 8.16 mm CL at Gardner Pinnacles, and 99.52 ± 8.98 mm CL at Maro Reef. Using a Kruskal–Wallis test, a significant difference in size distributions was found among banks ($\chi^2 = 617.13$, df = 2, $P < 0.0001$). Specifically, Kolmogorov–Smirnov tests indicated significant differences in size distributions between Necker Island and Gardner Pinnacles (Kolmogorov–Smirnov D-statistic = 0.49, $P < 0.0001$) and between Necker Island and Maro Reef ($D = 0.53$, $P < 0.0001$) but not between Gardner Pinnacles and Maro Reef ($D = 0.08$, $P = 0.69$). The size structure differences between Necker Island and the other banks were probably not due to sampling issues because the same trapping gear and sampling protocol were used during each tagging cruise.

Growth Model Results

The models containing g_α, g_β, s, and v resulted in the best fit to the von Bertalanffy growth model for all data sets (Table 3), and g_α, g_β, s, v, and b resulted in the best fit to the Schnute growth model (Table 4); introducing additional parameters did not result in a significant improvement in fit, as evident in the likelihood ratio tests.

To assess model fits, residuals and standardized residuals were plotted against length at release and predicted growth; a representative data set of the von Bertalanffy model (Necker Island 2003–2004 males) is shown in Figure 4. Both growth models displayed declining residuals with increasing length at release because mean growth declines with length (McGarvey et al. 1999), while residuals versus predicted growth showed the opposite trend, as would be expected. Standardized residuals (residuals divided by σ_i, which, in the selected model, equals s) showed no pattern, indicating that the model assumption that growth variability is dependent on mean growth was not violated (Francis 1988b). Residuals of all bank-, year-, and sex-specific data sets were generally symmetric around a mean of zero; the von Bertalanffy model residuals are shown in Figure 5. Overall, residual plots indicated satisfactory fits such that both models were suitable for the NWHI Hawaiian spiny lobster tagging data.

Both growth models generated similar estimates of

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

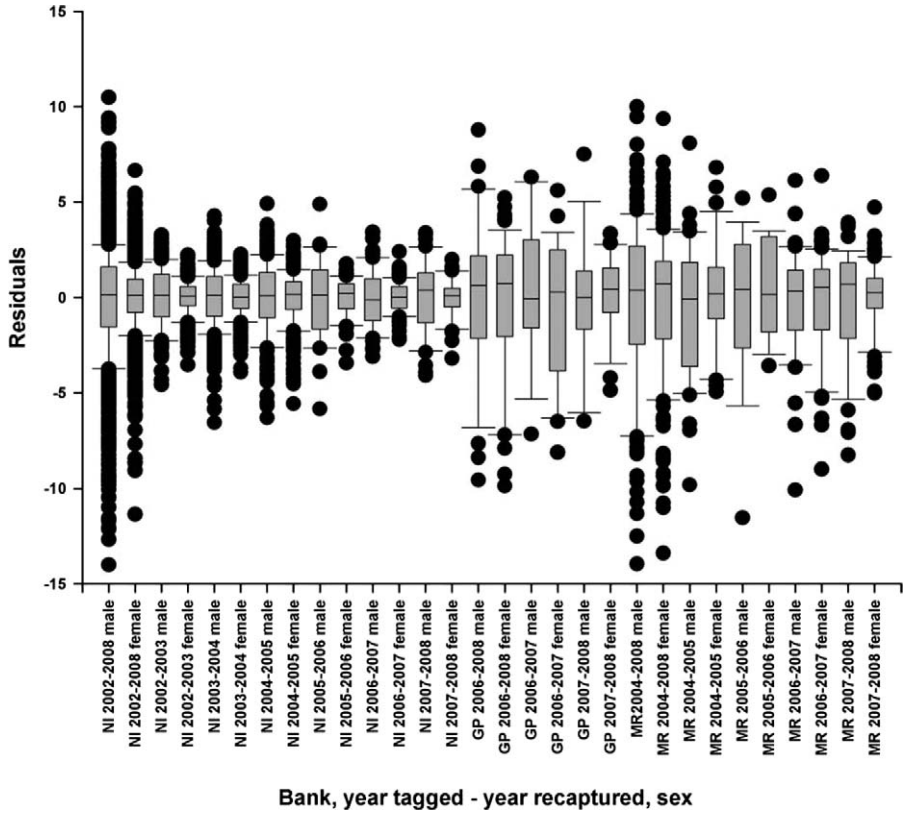


FIGURE 5.—Box-and-whisker plots of von Bertalanffy growth model residuals for Hawaiian spiny lobsters by bank (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef), study period (year tagged–year recaptured), and sex.

g_α, g_β, and v (Tables 5, 6). However, the von Bertalanffy growth model had lower AIC_c values relative to the Schnute growth model in 67% of the male data sets (Necker Island: 2002–2003, 2003–2004, 2005–2006, 2006–2007, 2007–2008; Gardner Pinnacles: 2006–2007, 2007–2008; Maro Reef: 2005–2006, 2006–2007) and 73% of the female data sets (Necker Island: 2003–2004, 2005–2006, 2006–2007, 2007–2008; Gardner Pinnacles: 2006–2007, 2007–2008, 2006–2008; Maro Reef: 2004–2005, 2005–2006, 2006–2007, 2007–2008) and is therefore considered the better model. All reported growth estimates are from the von Bertalanffy model.

Individual Variability and Mean Growth Rates

Hawaiian spiny lobsters exhibited substantial individual variability in growth, with the estimated v for all data sets ranging from 0.24 to 0.71 (Table 5). Estimates of g_{75} and g_{110} indicated that Hawaiian spiny lobsters displayed sexual dimorphism in growth, with males growing faster than females (Table 7). The estimated Hawaiian spiny lobster growth rates also indicated that male and female growth was consistently slowest at Necker Island (Table 7). In years when tagging took place at all three banks (2006–2007 and 2007–2008), Necker Island 75- and 110-mm CL males grew three times slower than those at Gardner Pinnacles and two times slower than those at Maro Reef. Female Hawaiian spiny lobsters exhibited the same pattern, but the differences between banks were slightly less pronounced. During the same time period, male and female Hawaiian spiny lobsters grew slightly faster at Gardner Pinnacles than at Maro Reef except for female g_{110} in 2007–2008. The slower growth trend of Necker Island lobsters was further confirmed by comparing growth rates between Necker Island and Maro Reef lobsters during the extended time series of 2004–2005 to 2007–2008. Plots of bootstrap growth estimates (Figure 6) and the nonoverlapping 95% CIs (Table 5) indicate that the differences between Necker Island and the other banks were significant. Although smaller, the difference in growth between Gardner Pinnacles and Maro Reef lobsters was also significant.

Temporal variability in Hawaiian spiny lobster

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 5.—Final von Bertalanffy model (Francis 1988a method) estimated growth parameters (95% confidence intervals in parentheses) for male and female Hawaiian spiny lobsters (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef; g_α = mean annual growth of α, where $\alpha = 75$ and 70 mm carapace length [CL] for males and females, respectively; g_β = mean annual growth of β, where $\beta = 110$ and 100 mm CL for males and females, respectively; v = coefficient of variation of growth variability; K = von Bertalanffy growth constant; and L_∞ = asymptotic maximum length). The SD of measurement error (s) included in the final model was fixed at 0.17 and 0.12 for males and females, respectively.

Bank	Year tagged–year recaptured	g_α, mm/year		g_β, mm/year	
		Male	Female	Male	Female
NI	2002–2003	3.70 (3.36–4.08)	2.28 (2.07–2.50)	1.78 (1.51–2.02)	0.56 (0.45–0.66)
	2003–2004	3.71 (3.53–3.89)	2.29 (2.15–2.44)	1.93 (1.72–2.11)	0.62 (0.50–0.73)
	2004–2005	4.75 (4.42–5.08)	3.18 (2.96–3.41)	1.57 (1.32–1.82)	0.91 (0.75–1.08)
	2005–2006	5.69 (4.70–6.71)	2.75 (2.41–3.16)	2.37 (1.51–3.17)	0.74 (0.36–0.91)
	2006–2007	4.60 (4.00–5.23)	2.48 (2.20–2.78)	2.31 (1.79–2.93)	0.51 (0.32–0.70)
	2007–2008	5.35 (4.61–6.05)	2.68 (2.25–3.12)	2.07 (1.25–2.88)	0.51 (0.25–0.78)
	2002–2008	4.42 (4.31–4.54)	2.51 (2.43–2.59)	1.81 (1.71–1.90)	0.71 (0.66–0.76)
GP	2006–2007	12.96 (10.83–15.58)	10.46 (8.38–12.79)	5.66 (4.48–6.85)	3.39 (2.71–4.02)
	2007–2008	14.86 (12.46–17.69)	8.65 (6.06–12.14)	1.71 (0.24–3.36)	2.21 (1.68–2.90)
	2006–2008	12.46 (10.88–14.31)	9.01 (7.39–10.95)	5.29 (4.24–6.33)	2.75 (2.29–3.31)
MR	2004–2005	16.22 (14.38–18.09)	15.06 (13.56–16.74)	4.02 (3.37–4.65)	1.9 (1.56–2.26)
	2005–2006	16.53 (13.38–20.17)	12.16 (9.00–15.45)	2.93 (1.44–4.07)	3.07 (2.40–3.76)
	2006–2007	10.45 (8.62–12.40)	10.48 (9.03–12.44)	3.38 (2.72–3.94)	2.4 (2.08–2.76)
	2007–2008	10.65 (8.95–12.32)	7.17 (6.13–8.36)	3.14 (2.54–3.75)	2.22 (1.96–2.49)
	2004–2008	12.36 (11.28–13.50)	8.43 (7.69–9.19)	3.53 (3.2–3.88)	3.05 (2.78–3.28)

growth was also evident within banks (Table 5). In particular, females at Maro Reef experienced a 19% decline in growth between lobsters at liberty from 2004–2005 to 2005–2006, a 14% decline in growth from 2005–2006 to 2006–2007, and a 35% decline in growth from 2006–2007 to 2007–2008 (Table 5). Plots of bootstrap growth estimates (Figure 7) and the nonoverlapping 95% CIs indicated that differences in the first and last intervals were significant (Table 5). Males at Maro Reef experienced a significant 37% decline in growth from 2005–2006 to 2006–2007 (Table 5; Figure 7). Hawaiian spiny lobsters at Necker Island did not experience a significant change in growth during the same time periods, but males displayed a 28% increase in growth and females displayed a 39% increase in growth from 2003–2004 to 2004–2005 (Table 5). The only significant change in Gardner Pinnacle lobster growth was a decrease in male g_{110} from 2006–2007 to 2007–2008 (Table 5).

TABLE 6.—Final Schnute model (Francis 1995 method) estimated growth parameters (95% confidence intervals in parentheses) for male and female Hawaiian spiny lobsters (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef; g_α = mean annual growth of α, where $\alpha = 75$ and 70 mm carapace length [CL] for males and females, respectively; g_β = mean annual growth of β, where $\beta = 110$ and 100 mm CL for males and females, respectively; v = coefficient of variation of growth variability; and b = curvature). The SD of measurement error (s) included in the final model was fixed at 0.17 and 0.12 for males and females, respectively.

Bank	Year tagged–year recaptured	g_α, mm/year		g_β, mm/year	
		Male	Female	Male	Female
NI	2002–2003	3.60 (3.12–4.05)	3.04 (2.59–3.53)	1.77 (1.48–2.04)	0.61 (0.48–0.73)
	2003–2004	3.68 (3.52–3.85)	2.34 (2.16–2.51)	2.14 (1.90–2.38)	0.66 (0.52–0.78)
	2004–2005	4.72 (4.37–5.05)	3.24 (3.00–3.51)	2.0 (1.63–2.35)	1.15 (0.93–1.38)
	2005–2006	5.21 (4.15–6.28)	2.99 (2.47–3.44)	3.40 (2.00–4.63)	0.71 (0.48–0.94)
	2006–2007	4.67 (3.98–5.29)	2.36 (1.97–2.73)	2.60 (1.67–3.25)	0.49 (0.28–0.68)
	2007–2008	4.99 (4.35–5.79)	2.77 (2.20–3.27)	1.91 (1.20–2.52)	0.54 (0.26–0.87)
	2002–2008	3.60 (3.12–4.05)	3.04 (2.59–3.53)	1.77 (1.48–2.04)	0.61 (0.48–0.73)
GP	2006–2007	14.46 (10.56–18.43)	11.02 (6.96–15.29)	4.80 (3.26–6.53)	2.95 (2.14–3.92)
	2007–2008	15.55 (12.70–19.71)	9.92 (3.25–20.42)	2.95 (−0.27–5.06)	2.06 (1.48–2.95)
	2006–2008	14.05 (11.89–16.59)	9.19 (6.37–12.54)	4.30 (3.43–5.37)	2.65 (2.07–3.22)
MR	2004–2005	17.61 (15.36–19.90)	14.44 (12.64–16.42)	3.42 (2.83–3.92)	1.89 (1.56–2.25)
	2005–2006	16.81 (12.87–21.26)	13.12 (6.90–20.61)	3.19 (1.57–4.65)	2.98 (2.18–3.91)
	2006–2007	13.38 (10.21–16.83)	11.04 (8.32–14.64)	3.10 (2.47–3.71)	2.21 (1.82–2.67)
	2007–2008	14.19 (10.76–17.46)	7.94 (5.38–10.70)	3.13 (2.56–3.73)	2.16 (1.87–2.48)
	2004–2008	14.58 (13.43–16.39)	15.12 (13.09–17.12)	3.17 (2.85–3.48)	5.96 (5.53–6.49)

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 5.—Extended.

Bank	Year tagged–year recaptured	v		K		L_∞, mm	
		Male	Female	Male	Female	Male	Female
NI	2002–2003	0.54 (0.48–0.60)	0.57 (0.50–0.64)	0.06	0.06	142.42	109.70
	2003–2004	0.47 (0.43–0.50)	0.54 (0.49–0.59)	0.05	0.06	147.75	111.09
	2004–2005	0.50 (0.45–0.56)	0.57 (0.51–0.63)	0.10	0.08	127.33	112.00
	2005–2006	0.48 (0.34–0.62)	0.51 (0.39–0.62)	0.10	0.07	135.04	110.98
	2006–2007	0.40 (0.32–0.47)	0.45 (0.37–0.54)	0.07	0.07	145.40	107.79
	2007–2008	0.37 (0.28–0.47)	0.45 (0.32–0.56)	0.10	0.07	132.06	107.10
	2002–2008	0.48 (0.46–0.49)	0.53 (0.51–0.56)	0.08	0.06	134.22	111.89
GP	2006–2007	0.37 (0.22–0.49)	0.54 (0.36–0.69)	0.23	0.27	137.16	114.35
	2007–2008	0.24 (0.13–0.29)	0.71 (0.45–0.93)	0.49	0.24	113.41	110.33
	2006–2008	0.36 (0.26–0.46)	0.67 (0.52–0.85)	0.23	0.23	135.85	113.20
MR	2004–2005	0.37 (0.28–0.46)	0.32 (0.23–0.39)	0.43	0.58	121.52	104.33
	2005–2006	0.36 (0.21–0.47)	0.49 (0.28–0.65)	0.49	0.36	117.55	110.13
	2006–2007	0.42 (0.32–0.52)	0.56 (0.43–0.68)	0.23	0.31	126.76	108.94
	2007–2008	0.41 (0.31–0.51)	0.54 (0.43–0.63)	0.24	0.18	124.67	113.45
	2004–2008	0.46 (0.40–0.52)	0.60 (0.53–0.67)	0.29	0.20	124.00	117.03

Density and Sea Surface Temperature Effects

Examination of density effects on Hawaiian spiny lobster growth by using individual growth rates was valid because of the near-equal time at liberty for all individuals at a given bank in a specific year; this removes the effect of time at liberty when comparing growth rates relative to density. String-specific trap CPUE ranged from 0.05 to 3.55 lobsters/trap at Necker Island and from 0.05 to 2.80 lobsters/trap at Maro Reef. At both banks and in all years except for 2 years at Necker Island (2005–2006, 2006–2007), there was a significant effect of release size on Hawaiian spiny lobster growth (Table 8). After correcting for release size, density was suggested to have a negative effect on growth at Necker Island in only one of the 6 years examined and no effect in any year at Maro Reef. The regression analysis indicated no effect of SST on growth of 75-mm ($P = 0.30$) and 110-mm CL ($P = 0.17$) Hawaiian spiny lobsters at Necker Island and Maro Reef from 2005

TABLE 6.—Extended.

Bank	Year tagged–year recaptured	v		b	
		Male	Female	Male	Female
NI	2002–2003	0.53 (0.47–0.60)	0.56 (0.49–0.62)	0.26 (−2.12–2.24)	5.73 (3.44–7.77)
	2003–2004	0.47 (0.43–0.50)	0.54 (0.50–0.59)	2.16 (0.97–3.12)	1.83 (0.30–3.06)
	2004–2005	0.49 (0.44–0.54)	0.56 (0.51–0.61)	4.11 (2.69–5.21)	3.28 (1.65–4.74)
	2005–2006	0.47 (0.33–0.59)	0.50 (0.39–0.59)	5.11 (0.78–9.64)	2.93 (0.28–5.09)
	2006–2007	0.40 (0.31–0.46)	0.45 (0.37–0.52)	3.08 (−0.99–5.64)	−0.05 (−3.22–2.38)
	2007–2008	0.36 (0.26–0.43)	0.44 (0.33–0.55)	−2.34 (−7.70–0.96)	1.89 (−1.73–4.75)
	2002–2008	0.54 (0.47–0.60)	0.56 (0.49–0.62)	0.26 (−2.12–2.24)	5.73 (3.44–7.77)
GP	2006–2007	0.34 (3.26–6.53)	0.56 (0.36–0.72)	3.88 (−0.72–8.66)	2.66 (−2.24–7.45)
	2007–2008	0.23 (0.11–0.30)	0.72 (0.42–1.05)	5.12 (−1.92–17.36)	2.93 (−8.75–12.75)
	2006–2008	0.30 (0.21–0.36)	0.72 (0.53–0.91)	4.67 (1.51–7.11)	1.50 (−1.71–4.09)
MR	2004–2005	0.34 (0.25–0.42)	0.31 (0.23–0.38)	5.35 (2.70–9.17)	−0.75 (−3.97–1.63)
	2005–2006	0.35 (0.22–0.48)	0.48 (0.28–0.64)	2.46 (−3.65–9.52)	3.47 (−5.09–11.68)
	2006–2007	0.40 (0.29–0.48)	0.58 (0.45–0.70)	4.72 (0.74–8.82)	2.30 (−1.25–5.78)
	2007–2008	0.36 (0.28–0.44)	0.53 (0.41–0.64)	7.17 (2.91–12.26)	2.12 (−1.62–4.83)
	2004–2008	0.41 (0.36–0.46)	0.45 (0.39–0.50)	5.37 (3.70–7.29)	2.07 (0.38–3.44)

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

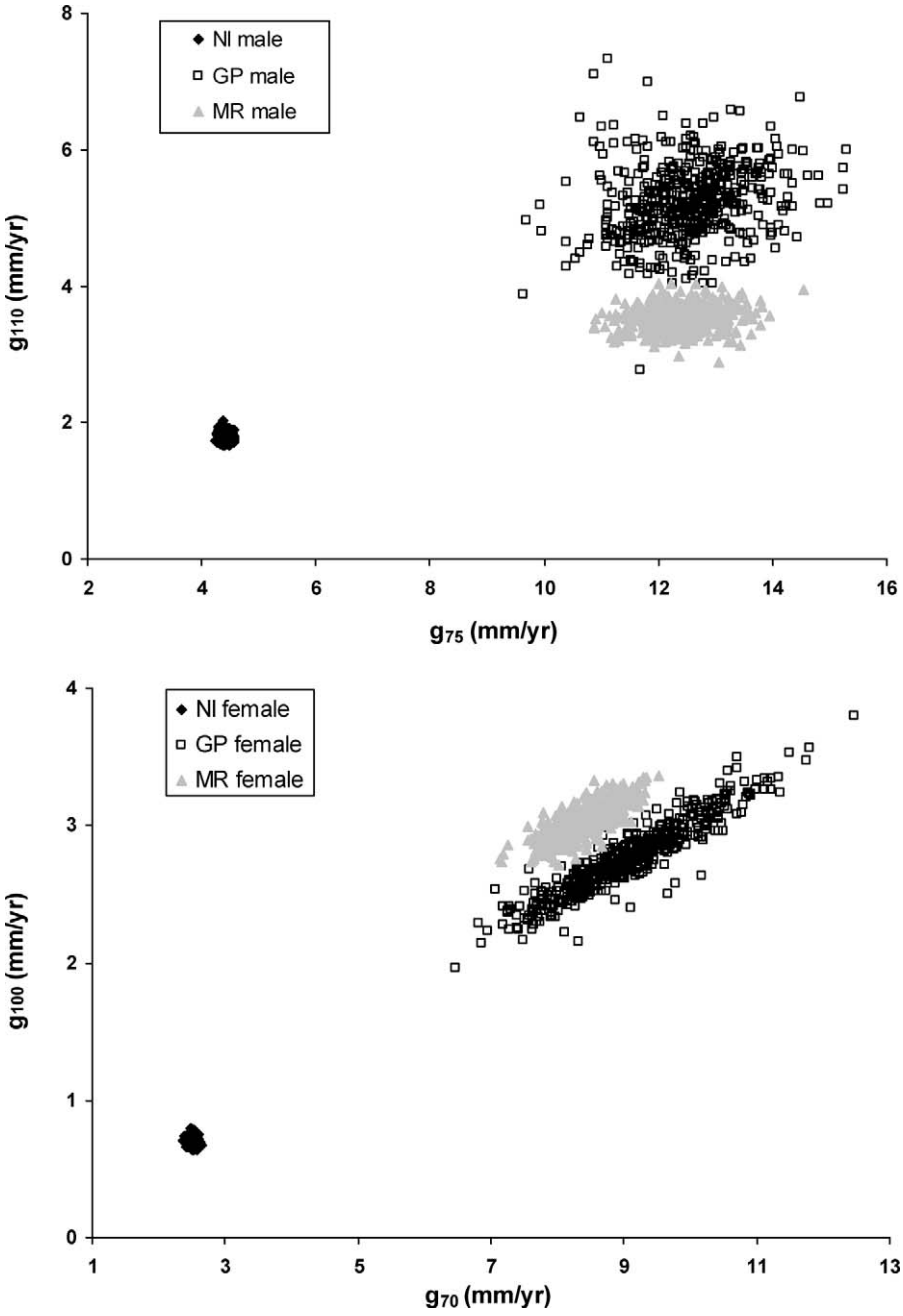


FIGURE 6.—von Bertalanffy growth model bootstrap estimates of growth (g; mm carapace length [CL]/year) for male (top; reference lengths = 75 and 110 mm CL) and female (bottom; reference lengths = 70 and 100 mm CL) Hawaiian spiny lobsters by bank for all years (NI = Necker Island, 2002–2008; GP = Gardner Pinnacles, 2006–2008; MR = Maro Reef, 2004–2008).

to 2008. The analysis also indicated significant effects of bank and sex on the growth rates of 75-mm (bank: $P < 0.001$; sex: $P = 0.004$) and 110-mm CL (bank: $P = 0.04$; sex: $P < 0.01$) lobsters, providing additional evidence of spatial and sexual variability in Hawaiian spiny lobster growth. Mean monthly averages of SST at Necker Island (mean ± SD = 25.6 ± 1.40°C) and Maro Reef (25.4 ± 1.83°C) were not significantly different from 2005 to 2008 (paired t-test: $P = 0.21$).

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

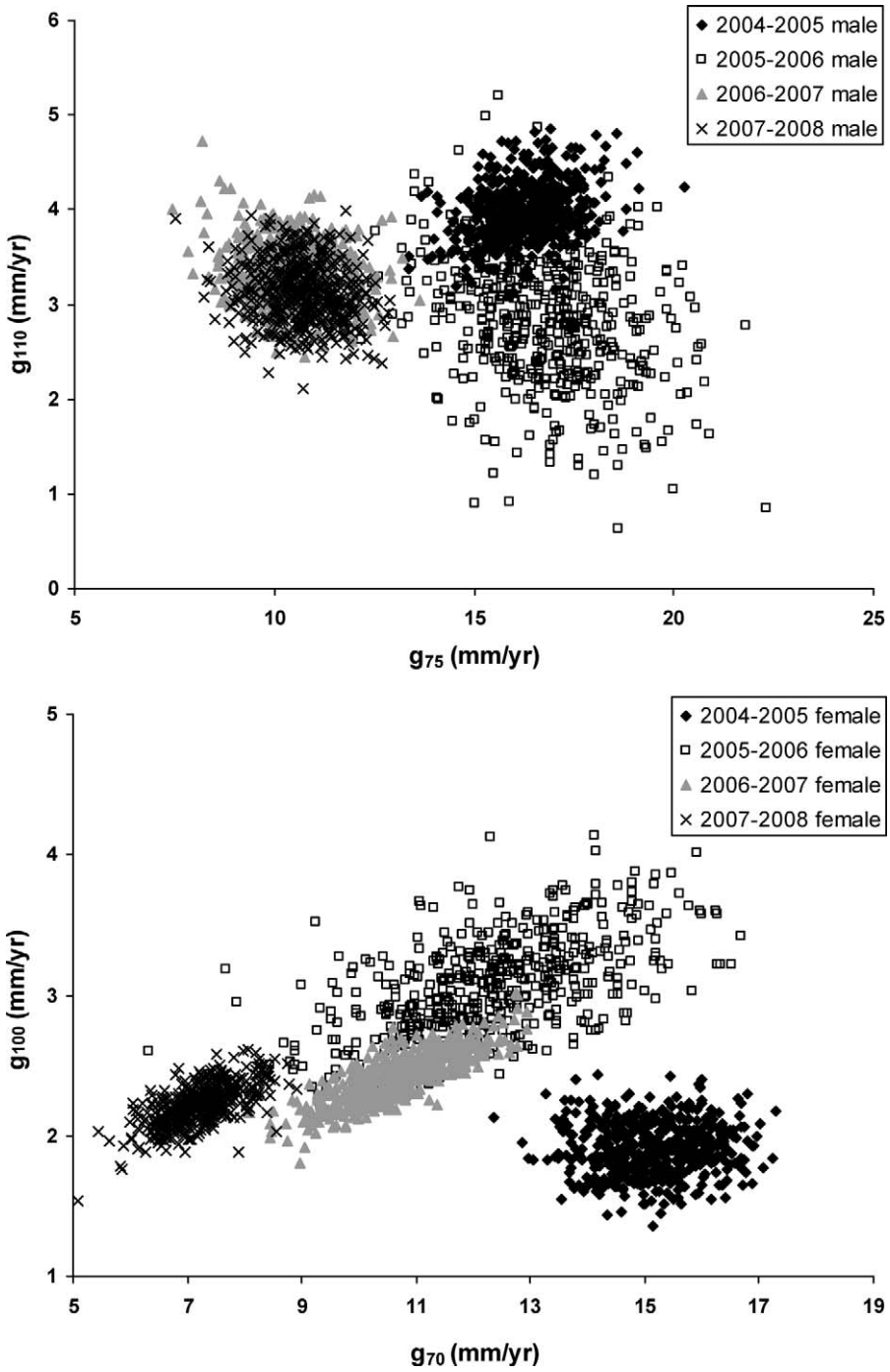


FIGURE 7.—von Bertalanffy growth model bootstrap estimates of growth (g; mm carapace length [CL]/year) for male (top; reference lengths = 75 and 110 mm CL) and female (bottom; reference lengths = 70 and 100 mm CL) Hawaiian spiny lobsters at Maro Reef, Northwestern Hawaiian Islands, 2004–2008.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 7.—Estimated mean annual growth of 75- and 110-mm (carapace length) male and female Hawaiian spiny lobsters (NI = Necker Island; GP = Gardner Pinnacles; MR = Maro Reef; g_{75} = mean annual growth of 75-mm lobsters; g_{110} = mean annual growth of 110-mm lobsters).

Bank	Year tagged–year recaptured	g_{75}, mm/year		g_{110}, mm/year	
		Male	Female	Male	Female
NI	2002–2003	3.70	1.99	1.78	0.00
	2003–2004	3.71	1.78	1.93	0.07
	2004–2005	4.75	2.80	1.57	0.15
	2005–2006	5.69	2.42	2.37	0.07
	2006–2007	4.60	2.15	2.31	0.00
	2007–2008	5.35	2.34	2.07	0.00
	2002–2008	4.42	2.21	1.81	0.11
GP	2006–2007	12.96	9.28	5.66	1.03
	2007–2008	14.86	7.58	1.71	0.08
	2006–2008	12.46	7.97	5.29	0.66
MR	2004–2005	16.22	12.87	4.02	0.00
	2005–2006	16.53	10.65	2.93	0.04
	2006–2007	10.45	7.12	3.38	1.34
	2007–2008	10.65	9.17	3.14	0.74
	2004–2008	12.36	7.53	3.53	1.26

Discussion

Model and Tagging Assumptions

A reparameterization of the von Bertalanffy growth model (Francis 1988a) and a mark–recapture analog of the Schnute growth model (Francis 1995) were used to examine spatial and temporal variability in growth of NWHI Hawaiian spiny lobsters. Although both model estimates of growth were similar and residual plots indicated that both were suitable for the Hawaiian spiny lobster tag–recapture data, the von Bertalanffy model was considered the preferred model based on AIC_c values. Palinurid growth has been adequately described by the von Bertalanffy model (Morgan 1980; Wahle and Fogarty 2006) and, more specifically, utilizing the GROTAG method (McGarvey et al. 1999; Montgomery et al. 2009). The Hawaiian spiny lobsters' small growth increments relative to maximum size allow use of the von Bertalanffy model despite the assumption of continuous growth (Frisch 2007; Montgomery et al. 2009). Further, decreasing growth with increasing size and the lack of extreme outliers, particularly at small and large sizes, indicate that this growth model is suitable for the Hawaiian spiny lobster. Biases in growth rates can arise when individuals with a higher probability of zero growth (short time at liberty) are included in the analysis. All data sets only included lobsters that had been at liberty for longer time periods, hence avoiding this source of bias. Individuals recaptured after a short time at liberty usually provide information for GROTAG to estimate measurement error. Fixing the model's measurement error parameters at values estimated independently still allowed the model to accurately estimate the growth parameters while excluding those individuals that were at liberty for shorter amounts of time.

An important assumption in tagging studies is that the tagging process does not significantly affect growth of tagged individuals relative to untagged individuals. Tag-induced effects were found in similar lobster species (Waugh 1981; Brown and Caputi 1985; Hunt and Lyons 1986). Despite taking precautions to minimize handling and exposure during the tagging process, it is impossible to disregard this assumption, although there is no evidence that the assumption was violated in this study. Even with the possibility of tag-induced effects occurring, it would not change the conclusion of growth variability because the exact tagging methodology replication spreads any bias evenly across banks and years, with the exception being Necker Island in 2002, when a different tag type was used.

TABLE 8.—Multiple regression analysis of the effects of Hawaiian spiny lobster density on individual-specific growth rates at Necker Island (NI; 2002–2008) and Maro Reef (MR; 2004–2008). Sources of variation are release size (carapace length at release, mm), catch per unit effort (CPUE; number of lobsters caught on the same string/trap; 20 traps/string) and the release size × CPUE interaction term (MS = mean square; SS = sum of squares; and df = degrees of freedom).

Bank	Year tagged–year recaptured	Effect											
		Release size			CPUE			Release size × CPUE			Error		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	df	SS	MS
NI	2002–2003	3.02	10.39	0.001	0.78	2.67	0.10	0.68	2.33	0.13	460	133.63	0.29
	2003–2004	2.26	8.64	0.003	0.001	0.005	0.95	0.0007	0.003	0.96	896	234.45	0.26
	2004–2005	17.13	54.14	<0.001	2.74	8.67	0.003	2.31	7.30	0.007	625	197.80	0.32
	2005–2006	1.15	3.04	0.08	0.12	0.32	0.57	0.13	0.32	0.57	100	37.87	0.38
	2006–2007	0.22	0.81	0.37	<0.001	<0.001	0.991	0.0005	0.002	0.97	161	44.17	0.27
	2007–2008	2.30	7.44	0.008	1.28	4.14	0.05	1.33	4.29	0.04	80	24.71	0.31
MR	2004–2005	13.32	26.49	<0.001	0.36	0.72	0.40	0.13	0.26	0.61	76	38.21	0.50
	2005–2006	3.36	6.69	0.01	0.22	0.44	0.51	0.32	0.63	0.43	35	17.58	0.50
	2006–2007	7.09	15.24	<0.001	0.31	0.66	0.42	0.43	0.92	0.34	105	48.83	0.47
	2007–2008	2.60	6.79	0.01	1.30	3.39	0.07	1.13	2.95	0.09	119	45.52	0.39

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Hawaiian Spiny Lobster Growth Rates in the Northwestern Hawaiian Islands

The estimated values of v indicate that the Hawaiian spiny lobster does exhibit substantial individual variability in growth, thus warranting the use of Francis' (1988a) method. Failure to explicitly account for individual variability in growth (i.e., assuming all individuals in a population grow according to fixed parameters) can result in biased mean growth estimates (Sainsbury 1980; Tyler and Rose 1994; Smith et al. 1997). The high values also indicate that such variability should be taken into account in future NWHI lobster assessments (Parma and Deriso 1990; Hampton 1991).

Significant differences in Hawaiian spiny lobster mean growth rates were found between sexes, among banks, and among years within the NWHI. Sexual dimorphism is common in palinurid growth (Aiken 1980), with males commonly growing faster (Hunt and Lyons 1986; McGarvey et al. 1999; Robertson and Butler 2003). The bank- and year-specific nature of the tag–recapture events in this study allowed for estimation of Hawaiian spiny lobster growth rates that included temporal and spatial variability. Spatial variability was particularly evident between Necker Island and the other banks. Spatial differences in growth rates have been observed in other palinurids (Newman and Pollock 1974; Joll and Phillips 1984; Pollock 1991; Skewes et al. 1997; McGarvey et al. 1999); however, at their extreme, the differences between the slowest- and fastest-growing individuals in those studies were less than the differences at the NWHI banks reported here. Temporal variability was evident to some extent within each NWHI bank, but several particularly abrupt increases and decreases in growth were found at Necker Island and Maro Reef. Temporal differences in growth similar to those observed in Hawaiian spiny lobsters were exhibited by South African Cape rock lobsters *Jasus lalandii* (Pollock et al. 1997).

The GROTAG method does allow for conversion of g_α and g_β into K and L_∞ for the sake of comparison with similar species. The wide range of K estimates prevents grouping of the NWHI Hawaiian spiny lobster, as a species, with any specific group of palinurids. The Hawaiian spiny lobsters at Gardner Pinnacles and Maro Reef grew at a rate similar to that of tropical palinurids, yet Necker Island lobsters grew at a rate more typical of temperate palinurids (Wahle and Fogarty 2006; Frisch 2007).

Density-dependent growth has been exhibited in other palinurids, including the southern rock lobster *J. edwardsii* (McGarvey et al. 1999) and Tristan rock lobster *J. tristani* (Pollock 1991). Hawaiian spiny lobster density-dependent growth was suggested by pre-exploitation surveys that documented smaller individuals but greater abundance at Necker Island relative to other banks in the NWHI (Uchida et al. 1980). Polovina (1989) concluded that density influenced NWHI Hawaiian spiny lobster population dynamics based on (1) a positive relationship between density (CPUE) and the ratio of total mortality (Z) to growth (K) among seven banks and (2) indications that changes in natural mortality and K occurred at Necker Island and Maro Reef after heavy exploitation. However, whether density dependence was operating on mortality, growth, or both was beyond the scope of that study. The current study did not find a significant influence of density on growth; density could not explain variability in growth at Necker Island, at Maro Reef, or between the two banks. Further, if density dependence was operating, the relatively slow growth of Hawaiian spiny lobsters at Necker Island would be associated with higher lobster densities, and a comparison of CPUEs between Necker Island and Maro Reef does not support this hypothesis. This theory also applies to density dependence within Necker Island. If density dependence was operating, fast growth would be expected in 2002–2008 because CPUE was lower relative to CPUE during the advent of the fishery (Figure 2). It now seems plausible that the smaller Hawaiian spiny lobsters observed at Necker Island in the pre-exploitation surveys (Uchida et al. 1980) were a result of the relatively slow growth rather than density dependence.

Direct temperature effects have been linked to growth variability in other palinurid species (Wahle and Fogarty 2006); however, growth variability of NWHI Hawaiian spiny lobsters was not associated with differences in temperature. Temperatures were very similar between Necker Island and Maro Reef during the span of this study, yet Hawaiian spiny lobster growth was not, further discounting temperature as the cause of growth differences between banks.

It also appears likely that the differences in Hawaiian spiny lobster growth between Necker Island and the other banks cannot be attributed to genetic differences. An analysis of allozyme frequencies prior to exploitation found a single panmictic stock throughout the Hawaiian Archipelago (Shaklee and Samollow 1984), and postexploitation analysis of allozyme frequencies in Necker Island and Maro Reef Hawaiian spiny lobsters found no differences in six out of seven loci (Seeb et al. 1990). It is also unlikely that the differences in growth among banks are a result of genetic selection for slower-growing individuals by the commercial fishery (Conover and Munch 2002) based on the

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

historically smaller Hawaiian spiny lobsters at Necker Island; the similar levels of exploitation at Necker Island, Gardner Pinnacle, and Maro Reef; and the lack of genetic structure in this species across the archipelago.

Because the slower growth of Hawaiian spiny lobsters at Necker Island cannot be explained by common drivers of variability (e.g., density, temperature, or genetics), the reason for the slower growth may be that a crucial dietary component of "normal" growth is missing at Necker Island. Temporal differences in Cape rock lobster growth were attributed to the collapse of their primary food source during the anomalous El Niño years of 1990–1993 (Pollock et al. 1997). Spatial variability in growth rates of juvenile western rock lobsters *Panulirus cygnus* was associated with local abundances of the top shell *Cantharidus lepidus*; western rock lobsters in the fast-growth areas ingested more top shells and less of the relatively nutritionally poor plant material than did lobsters in the slow-growth area (Edgar 1990).

The NWHI is a dynamic ecosystem that is poorly understood, and the factors that caused the growth differences between Necker Island and the other banks in the NWHI are, at this point, not readily identifiable. Future research should focus on aspects of the Hawaiian spiny lobster's diet, such as stable isotope analysis and nutritional indices (Parrish and Martinelli-Liedtke 1999), to help pinpoint the drivers of the growth variability. The variability in growth rates also suggests variability in other Hawaiian spiny lobster life history traits (e.g., mortality) as well as in life histories of other lobster species. The assumption that the scaly slipper lobster *Scyllarides squammosus*, an important component of the NWHI lobster fishery, also displays synchronous life history dynamics should now be examined. The results from such studies would not only provide species-specific information but would also provide insights into the dynamics of the NWHI ecosystem.

The results of this tagging study indicate that the assumption of homogenous Hawaiian spiny lobster population dynamics, a foundation of previous population assessments, is invalid. The application of growth rates estimated at one bank to other banks is likely inappropriate, as is the assumption of uniform annual growth within a given bank. A re-examination of the 1979–1983 Kure Atoll and French Frigate Shoals tagging data using the von Bertalanffy model fitted with the same maximum likelihood method employed here documented growth rates (Kure Atoll males: $g_{75} = 15.85$ mm/year, $g_{145} = 1.06$ mm/year; Kure Atoll females $g_{70} = 15.81$ mm/year, $g_{135} = 0.41$ mm/year; French Frigate Shoals males: $g_{75} = 11.84$ mm/year, $g_{110} = 5.01$ mm/year; French Frigate Shoals females: $g_{70} = 10.99$ mm/year, $g_{110} = 7.04$ mm/year; O'Malley and MacDonald 2009) that were similar to the contemporary Maro Reef and Gardner Pinnacles growth rates. The documented smallest average size of Hawaiian spiny lobsters at Necker Island from the pre-exploitation surveys (Uchida et al. 1980) also suggests that the slower growth rates exhibited by Necker Island lobsters in 2002–2008 are not a recent phenomenon. If, in the past, Hawaiian spiny lobsters at these banks grew at rates similar to those of contemporary populations, then the application of Necker Island growth rates to other banks was erroneous, as was applying Kure Atoll and French Frigate Shoals growth rates to Necker Island lobsters. Both were damaging in that (1) the Necker Island growth rates were significantly different from those at other banks and (2) because Necker Island was a focal point of the commercial fishery, the catch information contributed significantly to archipelago-wide assessments (Botsford et al. 2002).

Small differences in growth rates significantly affect outputs from population models (Jones 1979; Majowski et al. 1987; Lai and Gallucci 1988; Helser and Brodziak 1998). The identified spatial, temporal, and individual variability in growth of the Hawaiian spiny lobster lends credence to the possibility that ignoring variability in life history parameters introduced significant biases to previous NWHI lobster assessments. Recognition of and accounting for the mean and individual variability in a life history trait of this important endemic species will result in more accurate stock assessments and, ultimately, better understanding of lobster dynamics and the NWHI coral reef ecosystem.

Acknowledgments

A special thanks to the scientists who participated in the tagging cruises and to the captain and crew of the F/V *Marie M* and F/V *Katy Mary*. I also thank C. Simpfendorfer for providing a copy of GROTAG; M. Donohue and M. McCracken for statistical advice; and B. Kikkawa, F. Parrish, and R. Toonen for their thoughtful insights. Helpful comments were provided in reviews by B. Bowen, R. Blyth-Skyrme, D. Kobayashi, W. Walsh, and anonymous reviewers. Financial support was provided by the National Oceanic and Atmospheric Administration Cooperative Research Program and National Science Foundation Grant OCE06-23678 to Rob Toonen. This is Hawaii Institute of Marine Biology Contribution Number 1360. Northwestern Hawaiian Islands activity was conducted under permit numbers NWHICRER-2006-003, PMNM-2007-023, and PMNM-2008-044.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

References

Aiken, D. E. 1980. Molting and growth. Pages 91–163 *in* J. S. Cobb and B. F. Phillips, editors. The biology and management of lobsters, volume 1. Academic Press, New York.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Investigations Series II Marine Fisheries Great Britain Ministry of Agriculture Fisheries and Food 19.

Botsford, L., G. DiNardo, M. Fogarty, D. Goodman, and J. Hampton. 2002. Workshop proceedings on the development of spatially structured population models for Northwestern Hawaiian Islands lobster resources. National Marine Fisheries Service, Southwest Fisheries Science Center, Administrative Report H-02-01, Honolulu, Hawaii.

Brown, R. S., and N. Caputi. 1985. Factors affecting the growth of undersize western rock lobster, *Panulirus cygnus* George, returned by fishermen to the sea. U.S. National Marine Fisheries Service Fishery Bulletin 83:567–574.

Chittleborough, R. G. 1975. Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). Australian Journal of Marine and Freshwater Research 26:177–196.

Clark, W. G., S. R. Hare, A. M. Parma, P. J. Sullivan, and R. J. Trumble. 1999. Decadal changes in growth and recruitment of Pacific halibut (*Hippoglossus stenolepis*). Canadian Journal of Fisheries and Aquatic Sciences 56:242–252.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96.

Edgar, G. J. 1990. Predator-prey interactions in seagrass beds. I. The influence of macrofaunal abundance and size-structure on the diet and growth of the western rock lobster *Panulirus cygnus* (George). Journal of Experimental Marine Biology and Ecology 139:1–22.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Francis, R. I. C. C. 1988a. Maximum likelihood estimation of growth and growth variability from tagging data. New Zealand Journal of Marine and Freshwater Research 22:42–51.

Francis, R. I. C. C. 1988b. Are growth parameters estimated from tagging and age-length data comparable? Canadian Journal of Fisheries and Aquatic Sciences 45:936–942.

Francis, R. I. C. C. 1995. An alternative mark-recapture analogue of Schnute's growth model. Fisheries Research 23:95–111.

Frisch, A. J. 2007. Growth and reproduction of the painted spiny lobster (*Panulirus versicolor*) on the Great Barrier Reef (Australia). Fisheries Research 85:61–67.

Griffiths, D., and C. Harrod. 2007. Natural mortality, growth parameters, and environmental temperature in fishes revisited. Canadian Journal of Fisheries and Aquatic Sciences 64:249–255.

Haddon, M. 2001. Modelling and quantitative methods in fisheries. Chapman and Hall/CRC Press, Boca Raton, Florida.

Hampton, J. 1991. Estimation of southern bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertalanffy models incorporating individual variation. U.S. National Marine Fisheries Service Fishery Bulletin 89:577–590.

Helser, T. E., and J. K. T. Brodziak. 1998. Impacts of density-dependent growth and maturation on assessment advice to rebuild depleted U.S. silver hake (*Merluccius bilinearis*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 55:882–892.

Hunt, J. H., and W. G. Lyons. 1986. Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys. Canadian Journal of Fisheries and Aquatic Sciences 43:2243–2247.

Jeffery, J. A., and C. T. Taggart. 2000. Growth variation and water mass associations of larval silver hake (*Merluccius bilinearis*) on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 57:1728–1738.

Joll, L. M., and B. F. Phillips. 1984. Natural diet and growth of juvenile western rock lobsters *Panulirus cygnus* George. Journal of Experimental Marine Biology and Ecology 75:145–169.

Jones, R. 1979. An analysis of a *Nephrops* stock using length composition data. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 175:259–269.

Lai, H. L., and V. F. Gallucci. 1988. Effects of parameter variability on length-cohort analysis. Journal du Conseil International pour l'Exploration de la Mer 45:82–91.

MacDonald, C. D. 1984. Studies on recruitment in the Hawaiian spiny lobster, *Panulirus marginatus*. Pages 199–220 *in* R. W. Grigg and K. Y. Tanoue, editors. Proceedings of the second symposium on resource investigations in the Northwestern Hawaiian Islands. Miscellaneous Report UNIHI-SEAGRANT-MR-84-01. University of Hawaii Sea Grant College Program, Honolulu.

MacDonald, C. D., and J. S. Stimson. 1980. Population biology of spiny lobsters in the lagoon at Kure Atoll: preliminary findings and progress to date. Pages 161–174 *in* R. W. Grigg and R. T. Pfund, editors. Proceedings of the symposium on status of resource investigations in the Northwestern Hawaiian Islands. Miscellaneous Report UNIHI-SEAGRANT-MR-80-04. University of Hawaii Sea Grant College Program, Honolulu.

Majowski, J., J. Hampton, R. Jones, A. Laurec, and A. A. Rosenberg. 1987. Sensitivity of length-based methods for stock assessment: report of working group III. Pages 363–372 *in* D. Pauly and G. R. Morgan, editors. Length-based methods in fisheries research. International Center for Living Aquatic Resources Management (ICLARM) Conference Proceedings 13. ICLARM, Manila, and Kuwait Institute for Scientific Research, Safat.

McGarvey, R., G. J. Ferguson, and J. H. Prescott. 1999. Spatial variation in mean growth rates at size of southern rock lobster, *Jasus edwardsii*, in South Australian waters. Marine and Freshwater Research 50:333–342.

Montgomery, S. S., G. W. Liggins, J. R. Craig, and J. R. McLeod. 2009. Growth of spiny lobster *Jasus verreauxi* (Decapoda: Palinuridae) off the east coast of Australia. New Zealand Journal of Marine and Freshwater Research 43:113–123.

Morgan, G. R. 1980. Population dynamics of spiny lobsters. Pages 189–217 *in* J. S. Cobb and B. F. Phillips, editors.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The biology and management of lobsters, volume II. Academic Press, New York.

Newman, G. G., and D. E. Pollock. 1974. Growth of the rock lobster *Jasus lalandii* and its relationship to benthos. Marine Biology 24:339–346.

O'Malley, J. M. 2008. Evaluations of tag retention and a device for releasing discarded Hawaiian spiny lobsters *Panulirus marginatus*. North American Journal of Fisheries Management 28:619–624.

O'Malley, J. M., and C. D. MacDonald. 2009. Preliminary growth estimates of Northwestern Hawaiian Islands spiny lobster (*Panulirus marginatus*): indications of spatiotemporal variability. National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Administrative Report H-09-01, Honolulu, Hawaii.

Parma, A. M., and R. B. Deriso. 1990. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. Canadian Journal of Fisheries and Aquatic Sciences 47:274–289.

Parrish, F. A., and T. L. Martinelli-Liedtke. 1999. Some preliminary findings on the nutritional status of the Hawaiian spiny lobster (*Panulirus marginatus*). Pacific Science 53:361–366.

Pollock, D. E. 1991. Spiny lobster at Tristan da Cunha, South Atlantic: inter-island variations in growth and population structure. South African Journal of Marine Science 10:1–12.

Pollock, D. E., A. C. Cockcroft, and P. C. Goosen. 1997. A note of reduced rock lobster growth rates and related environmental anomalies in the Southern Benguela, 1988–1995. South African Journal of Marine Science 18:287–293.

Pollock, D. E., and L. V. Shannon. 1987. Response of rock-lobster populations in the Benguela ecosystem to environmental change: a hypothesis. South African Journal of Marine Science 5:887–899.

Polovina, J. J. 1985. Status of stocks of spiny lobsters at Necker Island and Maro Reef. National Marine Fisheries Service, Southwest Fisheries Science Center, Administrative Report H-85-12, Honolulu, Hawaii.

Polovina, J. J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Canadian Journal of Fisheries and Aquatic Sciences 46:660–665.

Polovina, J. J., and R. Moffitt. 1989. Status of lobster stocks in the Northwestern Hawaiian Islands, 1988. National Marine Fisheries Service, Southwest Fisheries Science Center, Administrative Report H-89-3, Honolulu, Hawaii.

Robertson, D. N., and M. J. Butler, IV 2003. Growth and size at maturity in the spotted spiny lobster, *Panulirus guttatus*. Journal of Crustacean Biology 23:265–272.

Sainsbury, K. J. 1980. Effect of individual variation on the von Bertalanffy growth equation. Canadian Journal of Fisheries and Aquatic Sciences 37:241–247.

Schenker, N., and J. F. Gentleman. 2001. On judging the significance of differences by examining overlap between confidence intervals. American Statistician 55:182–186.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Canadian Journal of Fisheries and Aquatic Sciences 38:1128–1140.

Seeb, L.W., J. E. Seeb, and J. J. Polovina. 1990. Genetic variation in highly exploited spiny lobster *Panulirus marginatus* populations from the Hawaiian Archipelago. U.S. National Marine Fisheries Service Fishery Bulletin 88:713–718.

Shaklee, J. B., and P. B. Samollow. 1984. Genetic variation and population structure in a spiny lobster, *Panulirus marginatus* in the Hawaiian archipelago. U.S. National Marine Fisheries Service Fishery Bulletin 82:693–702.

Sheehy, M. R. J. 2001. Implications of protracted recruitment for perception of the spawner-recruit relationship. Canadian Journal of Fisheries and Aquatic Sciences 58:641–644.

Simpfendorfer, C. A. 2000. Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag–recapture data. U.S. National Marine Fisheries Service Fishery Bulletin 98:811–822.

Skewes, T. D., C. R. Pitcher, and D. M. Dennis. 1997. Growth of ornate rock lobsters, *Panulirus ornatus*, in Torres Strait, Australia. Marine and Freshwater Research 48:497–504.

Smith, E. B., F. M. Williams, and C. R. Fisher. 1997. Effects of intrapopulation variability on von Bertalanffy growth parameter estimates from equal mark-recapture intervals. Canadian Journal of Fisheries and Aquatic Sciences 54:2025–2032.

Tyler, J. A., and K. A. Rose. 1994. Individual variability and spatial heterogeneity in fish population models. Reviews in Fish Biology and Fisheries 4:91–123.

Uchida, R. N., J. N. Uchiyama, D. T. Tagami, and P. M. Shiota. 1980. Biology, distribution, and estimates of apparent abundance of the spiny lobster, *Panulirus marginatus* (Quoy and Gaimard), in waters of the Northwestern Hawaiian Islands: Part 2. Size distribution, legal to sublegal ratio, sex ratio, reproductive cycle, and morphometric characteristics. Pages 131–142 *in* R. W. Grigg and R. T. Pfund, editors. Proceedings of the symposium on status of resource investigations in the Northwestern Hawaiian Islands. Miscellaneous Report UNIHI-SEAGRANT-MR-80-04. University of Hawaii Sea Grant College Program, Honolulu.

Wahle, R. A., and M. J. Fogarty. 2006. Growth and development: understanding and modeling growth variability in lobsters. Pages 1–44 *in* B. F. Phillips, editor. Lobsters: biology, management, aquaculture, and fisheries. Blackwell Scientific Publications, Oxford, UK.

Wahle, R. A., L. S. Incze, and M. J. Fogarty. 2004. First projections of American lobster fishery recruitment using a settlement index and variable growth. Bulletin of Marine Science 74:101–114.

Waugh, G. T. 1981. Management of juvenile spiny lobsters (*Panulirus argus*) based on estimated biological parameters from Grand Bahama Island, Bahamas. Proceedings of the Gulf and Caribbean Fisheries Institute 33:271–289.

Welsford, D. C., and J. M. Lyle. 2005. Estimates of growth and comparisons of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*). U.S. National Marine Fisheries Service Fishery Bulletin 103:697–711.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use