Stock-Recruitment-Environment Relationship in a *Portunus pelagicus* Fishery in Western Australia

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**Abstract**

Blue swimmer crab (*Portunus pelagicus*) fisheries in Western Australia have generally been considered robust to recruitment overfishing, as the minimum legal size for retention of these crabs in both the commercial and recreational crab fisheries are set well above the size at sexual maturity allowing crabs to spawn at least once before entering the fishery. However, the Cockburn Sound crab stock suffered a recruitment collapse, with three key factors: (a) the fishery is near the edge of this species distribution and hence vulnerable to environmental fluctuations; (b) a number of consecutive years of poor environmental conditions resulted in poor recruitments; and (c) high fishing pressure continued on these low recruitments. This study indicates that water temperatures at the start of the spawning season positively influence the strong stock-recruitment relationship for *P. pelagicus* in Cockburn Sound. Apparently, warm water temperatures at the onset of spawning result in the larger females producing additional broods of eggs, and therefore a far greater number of larvae over the short spawning season. This relationship produces catch predictions for this fishery a year ahead and provides information for the development of biological reference points for management.
Introduction

Large interannual variations in population size are common among crustaceans (Lipcius and van Engel 1990, Metcalf et al. 1995, Wahle et al. 2004). For those species that support fisheries, variation in population size is typically reflected in significant fluctuations in landings, which create uncertainty for managers and may consequently have an adverse effect on the livelihoods of commercial fishers (Zheng and Kruse 1999, Bellchambers et al. 2006).

Year-to-year variations in stock size are largely attributed to variations in recruitment (both larval and the emigration of adults) and fishing mortality (the removal of older, larger animals) (Ricker 1954, Beverton and Holt 1957). Although successful larval recruitment is reliant on adequate spawning biomass, the strength of this is usually influenced by various physical or biotic factors affecting the survivorship of both larval and juvenile stages prior to and after settlement (Cobb and Caddy 1989, Wahle 2003). For example, successful settlement of western rock lobster (Panulirus cygnus) pueruli along the coast of Western Australia is dependent on climatic conditions such as warm water temperatures, which influence growth/survival, and winds favorable to the transport of larvae toward the coast prior to settlement (Caputi et al. 2001).

Other environmental variables demonstrated to affect the survivorship and recruitment of decapods include water temperature (McConaugha et al. 1983), salinity (Anger et al. 1998), turbidity (Penn and Caputi 1986), habitat availability (Botero and Atema 1982), and oceanographic processes, including tidal velocities and prevailing currents (Goodrich et al. 1989, Caputi et al. 1995, Rabalais et al. 1995, Lee et al. 2004, Queiroga et al. 2006). Although recruitment may be influenced by any one of these environmental variables, the ability to model the relationship, and the relevance of the relationship to the management of the fishery, will be dictated by the strength of the recruitment correlation (Walters and Collie 1988, Basson 1999).

Water temperature has been implicated as an important factor in the majority of the recruitment-environment relationships and is often robust enough to persist over substantial time frames (Caputi et al. 1995, Uphoff 1998). This is particularly true of stocks located near the latitudinal limit of species distributions, where water temperatures can be outside the optimal range for successful recruitment (Myers 1998). Water temperature may affect recruitment in a variety of ways. For example, elevated water temperatures typically have a positive effect on decapod recruitment by accelerating larval development and reducing the duration of the larval phase and larval mortality (Bryars and Havenhand 2006, Fisher 2006). Elevated water temperatures prior to spawning may also directly affect the timing of larval release by
controlling gonad development, mating, and the timing of spawning (Rosenkranz et al. 2001) as well as the larval habitat through changes to the abundances of larval foods and predators.

The blue swimmer crab (*Portunus pelagicus* [Linnaeus]) is distributed throughout the shallow marine and estuarine waters of the Indo-Pacific. Although predominantly a tropical or subtropical species, *P. pelagicus* is also found as far south as the temperate waters of southern Australia and differing environments throughout its large latitudinal range (26ºN–34ºS) have a major influence on its reproductive biology. de Lestang et al. (2003a) demonstrated that the spawning season of *P. pelagicus* in Shark Bay, where water temperatures remain above 18ºC for a substantial part of the year, is considerably more protracted (spawns year-round) than in the temperate waters of Cockburn Sound where the spawning season is restricted to spring and summer. They suggested that water temperatures have a significant influence on egg production in blue swimmer crabs, and therefore the timing and longevity of the spawning period. Additionally, in the temperate waters of South Australia, Bryars and Havenhand (2006) demonstrated increased survivorship of *P. pelagicus* larvae at temperatures over 19ºC and concluded that post-larval settlement would be greatest during abnormally warm summers. This highlights the influence water temperature can have on the life cycle of these crabs. It can affect the timing of spawning, which influences egg release times and the environment into which the larvae are released. Water temperatures during the larval cycle dramatically influence the length of larval life and therefore survival and the timing of juvenile recruitment, which can then impact on the ability of juvenile crabs to mature and mate the following year (Yatsuzuka 1962). Therefore, water temperatures during one only part of the life cycle can significantly alter population size and structure over a far greater timeframe.

Cockburn Sound, situated 30 km southwest of Perth, Western Australia (WA), was the second largest of the four main blue swimmer crab fisheries in WA. Commercial catch of blue swimmer crabs from Cockburn Sound is characterized by high interannual variability, ranging between 84 and 362 t from 1989/90 to 2004/05. Cockburn Sound, which is close to the Perth metropolitan area, also supports an important recreational crab fishery. Recreational surveys in the last 10 years have indicated an annual catch between 18 and 23 t. Although the variability in catch has been attributed to recruitment success (Belchambers et al. 2006), the specific factors responsible for variation in recruitment strength have yet to be identified.

Blue swimmer crab fisheries in Western Australia have generally been considered robust to recruitment overfishing as the minimum legal size for the Cockburn Sound fishery for both the commercial and recreational crab fishery (130 and 127 mm carapace width [CW], respec-
tively) are set well above the size at sexual maturity (98 mm CW) allowing crabs to spawn at least once before entering the fishery (de Lestang et al. 2003). However, an extremely low catch (53 t) from high levels of effort in 2005/06, which signified high exploitation and the possibility of recruitment-overfishing, prompted managers to close the Cockburn Sound fishery for three seasons (2006/07, 2007/08 and 2008/09). The impact a management response such as this can have on the livelihoods of fishers and recreational interests of fishers highlights the pressing need for understanding the cause of the recruitment decline and improved management of the fishery.

The aim of the present study was to determine the combination of spawning stock and environmental effects that contributed to the collapse of this seemingly robust stock to enable an assessment of whether other similar fisheries may also be vulnerable.

**Methods**

**Study site**

Cockburn Sound (32.10ºS, 115.43ºE) is an embayment about 15 km long by 10 km wide and around 100 km² in area (Fig. 1).

**Fishery-independent sampling**

Crabs were sampled in Cockburn Sound using a small otter trawl net (tri-net), which was 5 m wide, 0.5 m high, and 5 m long, and had 51 mm mesh in the wings and 25 mm mesh in the bunt. The bridle was 13 m long, while the warp length was varied with water depth according to the equation, warp length = water depth × 3.5. For each replicate trawl, the net was towed at a speed of 3.5 km per hour for a distance of 750 m. A net efficiency factor was incorporated to adjust the effective spread of the net on the seabed (0.6 × net headrope length in meters) (de Lestang et al. 2003c). The area trawled at each site was then calculated by multiplying the distance covered by the effective net spread (de Lestang et al. 2003b). The otter trawl was used to collect *P. pelagicus* from three randomly spaced replicate sites in each of three separate areas of Cockburn Sound—the northern, middle, and southern portions of this embayment (Fig. 1), between April 1998 and May 2008. Although the sampling program was conducted in two separate periods due to changes in funding, the methodology and sampling was kept consistent to make the results comparable between the periods. The first sampling period was between April 1998 and March 2000 when sampling was conducted during hours of daylight on a monthly basis. The second sampling period was January to May in the seven years between 2002 and 2008 when each site was trawled both during the day and at night on a fortnightly basis. Each site was 1,000 m × 250 m
and was oriented in a southwest-northeast direction to accommodate local weather and sea conditions. The substrate at each site consisted of sparsely vegetated sand and silt, in depths ranging between 17 and 24 m. Additional fishery-independent trawl samples of *P. pelagicus* were obtained from opportunistic sampling conducted annually using a research trawler with twin 20 fm nets.

The carapace width (CW), the distance between the tips of the two lateral spines of the carapace, of each crab was recorded to the nearest millimeter. In addition, the crabs were sexed and the presence or absence of eggs recorded (see de Lestang et al. 2003a for more details).

**Commercial catch monitoring**

Monitoring of the commercial catch began in January 1999 and continued until June 2006. During this program, research staff joined three commercial “crab-trapping” vessels (represents approximately 20% of the fleet) for a day in each month of the fishing season (December-
September) to record details of the catch. When commercial fishing ceased in late 2006 due to the closure of the fishery, “commercial” catch monitoring was continued (since January 2007) via the charter of commercial vessels. These vessels were directed to fish in their normal pattern, and their catch was monitored and subsequently returned to the water.

**Standardized egg production index**

An index of egg production (EPI) for Cockburn Sound was developed using data derived from the three sampling methods (small and large research survey trawls and commercial trap-based sampling). An index of egg production is the most appropriate measure of breeding stock abundance as it directly relates to the abundance of eggs/larvae produced by the stock. Measures such as female abundance fail to account for the nonlinear relationship between crab size and eggs produced.

Each female crab captured during fishery-independent trawling and commercial crab-trap sampling was assigned a total potential egg production based on a batch frequency (Bfr) to CW relationship (\(Bfr = 1+2/[1+\exp(-\log[19](CW-113.7)/13.8)]\)) and a batch fecundity (Bfe) relationship (\(Bfe = 1.821\log(CW)+3.2862\)) (de Lestang et al. 2003a). For example, the above equations estimate a 100 mm CW female *P. pelagicus* will produce an average of 1.12 batches of eggs, each totaling 117,270 eggs in a spawning season, which equates to a total potential egg production of 129,230 eggs per season. This relationship was used to convert female catch rates (female crabs per m\(^2\) trawled or per potlift, depending on the survey method) into potential egg catch rates (eggs per m\(^2\) trawled or per potlift). A generalized linear model (GLM) was then used to produce a seasonal (July-June) potential egg catch rate estimate (EPI) (a GLM was used to standardize for an unbalanced sampling design and sampling methodology). The samples were also restricted to water depths ≥15 m, since the majority of breeding sized females are found in these water depths (Potter et al. 2001). The average egg production per sample (per m\(^2\) or per trap) was log transformed to remove skewness from the data (Clark and Warwick 2001). Method of capture (small and large research trawl and crab trap), season, and month were treated as factors in the GLM with all two-way interactions. Back transformation of least-squares means of the seasonal estimates were used as the standardized EPI.

**Water temperature**

The monthly water temperature data incorporated into the stock-recruitment relationship was recorded at Warnbro Sound (10 km southwest of Cockburn Sound) as part of a survey of western rock lobster *Panulirus cygnus* recruitment conducted since 1984. Two replicate water temperature measurements are collected monthly using a mercury thermometer.
from a boat in a standard location toward the center of the embayment at a depth of about 2 m. For the few years when both measurements are available Warnbro Sound water temperatures were found to be very similar to those experienced by crabs in Cockburn Sound ($r^2 = 0.86$, $P < 0.001$, d.f. = 31, data not shown).

**Stock-recruitment relationship**

A modified Beverton and Holt (1957) stock-recruitment equation, $\text{Catch} = \frac{(EPI \times \exp[W\text{temp} \times -a])/(b+c \times EPI)}{b+c}$, was used to describe the relationship between spawning stock ($EPI_{t+1}$), subsequent recruitment strength ($\text{commercial catch}_{t+1/t+2}$), and water temperatures ($W\text{temp}$) just before, during and after peak egg production, i.e., May$_t$ to April$_{t+1}$. Commercial catch was used as a proxy for recruitment strength since the seasonal commercial catch (December to September) is mainly derived from a single 1+ year class (de Lestang et al. 2003b, Bellchambers et al. 2006). Although CPUE in the Cockburn Sound commercial blue swimmer crab fishery has followed similar patterns to total landings during recent years (Fig. 2), the use of annual landings as a measure of crab abundance was considered more appropriate than CPUE. This is because the fishery underwent major gear and effort changes in the early 1990s, and as such a consistent CPUE measure cannot be determined. Commercial catch on the other hand was considered a good proxy of settlement one year previously, since the legal population (mainly 1 year old crabs) are substantially depleted each fishing season to the point that fishing becomes no longer economically viable.

The relationship between spawning stock, recruitment, and water temperature in months before, during, and after peak egg production
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Figure 3. (a) Mean monthly water temperatures (solid line) (±1SD, dotted lines) from Warnbro Sound between 1996 and 2008. (b) Mean monthly percentage (+1SD) of ovigerous female *Portunus pelagicus* among all adult female *P. pelagicus* collected in Cockburn Sound from depths >15 m. Means are collated from research trawl samples and commercial catch monitoring data.

(and combinations of these months) was examined and the resultant $r^2$ values were examined to determine which of the monthly water temperatures (or combinations of months) have the strongest relationship with egg production and catch.

**Results**

The mean monthly water temperature cycle in Warnbro Sound (between 1996 and 2008) was lowest (16.1°C) in August, after which water temperature rose through spring and early summer to a maximum of 23.6°C in January (Fig. 3a). The mean percentage of female *Portunus pelagicus* that were ovigerous in any month demonstrates that the majority of reproductive activity in Cockburn Sound occurs during spring and summer, with the mean percentage of ovigerous crabs peaking in October and remaining high (>40%) until January (Fig. 3b).

Although the annual egg production index (*EPI*), which is a proxy for the size of the spawning stock each year, and the recruitment to the
Figure 4. Coefficient of determination ($r^2$) between observed stock (egg production index) and recruitment (commercial catch) and the fitted the Beverton and Holt stock-recruitment relationship, using egg production and commercial catch (recruitment) of the following year, and water temperatures in different months, or combinations of months, near the spawning and larval period.

Fishery (commercial catch) each season have both shown a general decline over the study period, fluctuations in $EPI$ values alone explain little of the annual variation in subsequent commercial catches ($r^2 = 0.36$, $P = 0.05$, d.f. = 9). The incorporation of water temperatures from individual months during the early to mid spawning season into the stock-recruitment relationship (SRR) increased the fit of the model substantially. The best fit explained approximately 76% of the variation in the catches and was produced by using August water temperatures in the model (Fig. 4), although good fits were generally obtained for months, August to December. In addition to the individual months, average water temperatures for various combinations of months from August to December were also evaluated in the SRR. The $r^2$ derived from the SRR of the mean water temperature during each of the combinations of months tested was greater than for August alone (Fig. 4) and the best correlation ($r^2 = 0.94$, $P < 0.001$, d.f. = 9) was derived from using the average water temperature in August and September during the commencement of spawning (Fig. 5). The relationship between water temperature in individual months (and an average of months) and commercial catch without incorporating $EPI$ in the model was also examined and the best relationship was not statistically significant ($r^2 = 0.26$, $P = 0.09$, d.f. = 9).

The strong influence of water temperature on the successful recruitment of crabs is demonstrated during the last decade, as the fishing seasons in which commercial landings were largest, i.e., 1997/98 and 1999/00 followed years 1996 and 1998, respectively, in which August/September water temperatures were elevated
Figure 5. Beverton and Holt stock-recruitment relationship between commercial catch and egg production (preceding season) at three different water temperatures (mean August/September), i.e., 16.0, 16.5, and 17.0°C. Year (fishing season) and mean temperature during the preceding August and September (in parentheses) are indicated. Open circles represent estimated commercial catches for 2006/07, 2007/08, and 2008/09 seasons based on recruit-catch relationship developed by D.J. Johnston et al. (pers. comm.).

Figure 6. Mean water temperatures (solid line) for August-September recorded in Warnbro Sound for the period 1996-2008. The average August-September water temperature (16.6°C) for the entire period is also indicated (dotted line).
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(>17°C) and the levels of egg production were moderate (Fig. 5). In contrast, when the mean August/September water temperatures were <16°C, e.g., 2003 and 2004, subsequent commercial landings in 2004/05 and 2005/06, respectively, were reduced, irrespective of the degree of egg production in the previous year (Fig. 5). Historically, the mean August/September water temperature in Warnbro Sound has fluctuated around the long-term average of 16.6°C, reaching a low of 15.7°C and a high of 17.7°C (Fig. 6). However, in recent years (2002-2005), mean August/September water temperatures remained below the long-term average for four consecutive years.

The initial reduction in catch in 2003/04 and 2004/05 appears to be mainly due to the environmental conditions (low water temperatures in 2002 and 2003), as the spawning stocks in the previous years (2002/03 and 2003/04) were at moderate levels (Fig. 5). The low recruitment to the fishery in these years, combined with fishing pressure, resulted in low levels of egg production in 2004/05. The subsequent low catch observed in 2005/06 along with the predicted low catches for 2006/07, 2007/08, and 2008/09 (based on juvenile abundance) may be due to the effect of low egg production.

The proportion of female crabs that are ovigerous in each month exhibit a similar annual pattern, increasing rapidly from a very low proportion in July and August to a peak two months later of between 0.5 and 0.9 in October (Fig. 7). Proportions remain high until January and then decline to essentially zero from March to June. Although this pattern remains similar between years, the magnitude of the proportions in a given month differ markedly following either a warm (>16.9°C) or cool (<16.3°C) mean August/September water temperature period (±0.3°C of the long term average 16.6°C). The most marked example of this is shown by the multiple spawning females (CW > 115 mm, see de Lestang et al. 2003a), with their proportions of ovigerous females being far greater (in some cases double) following a warm than cool August/September period (Fig. 7).

Discussion

We have demonstrated the importance of including environmental conditions (temperature) in the development of the SRR for blue swimmer crab in Cockburn Sound. Stock size alone, indexed by the EPI, explained a small proportion of the variance in recruitment ($r^2 = 0.36$). Similarly water temperature alone ($r^2 = 0.26$) was insufficient to explain recruitment. The poor recruitments, which occurred from 2004 to 2006, appears to be the result of high level of exploitation (D.J. Johnston et al. pers. comm.), on a series of low recruitments that initially occurred due to poor environmental conditions. There is a strong correlation between water temperatures and recruitment success of P. pelagicus in Cockburn
Figure 7. Variation in monthly proportions of small (CW 85-115 mm) and mainly single-brood producing females, and large (CW ≥ 115 mm) mainly multiple-brood producing females, following warm (>16.7°C) and cool (<16.1°C) August-September periods.

Sound, after taking into account the effect of the breeding stock. The marked influence of water temperatures on crab recruitment is not unexpected considering the tropical affinities of *P. pelagicus* and location of Cockburn Sound in the temperate waters of Western Australia. Bryars and Havenhand (2006) demonstrated that water temperature has an important influence on *P. pelagicus* larval duration and survival and predicted that post-larval settlement in the temperate waters of South Australia would be greatest during abnormally warm summers.

While water temperatures encountered by developing larvae in Cockburn Sound may influence larval survival and subsequent recruitment success, analysis of the $r^2$ values from the model demonstrate that water temperatures between August and December, i.e., at the beginning and during the spawning period, are more indicative of successful crab recruitment in the following year. This relationship suggests that recruitment success depends on a relationship between water temperature and the timing/magnitude of spawning.

The timing of spawning (more eggs released earlier) may contribute to strong recruitment in a number of ways. For example, early spawning may result in larvae being released at a time that allows them to take advantage of the particular food resources available at that time (e.g., Fisher 2006). It may also allow the larvae and subsequent juveniles more
In addition, an early start to spawning or a greater proportion of mature females spawning at the beginning of the spawning season may lead to an increase in the total number of juvenile crabs produced by providing female crabs the opportunity to produce, incubate and hatch their maximum number (three) of egg batches (de Lestang et al. 2003a). Without prolonged periods of favourable conditions it is unlikely that female crabs will mature early enough, reach an adequate size or have sufficient time to hatch this many batches of eggs. The far greater proportion of large ovigerous females following a warm rather than a cool August/September indicates that these females carried an extra batch of eggs in these years, which supports the above scenario.

The apparent role of high fishing pressure during periods of low recruitment bring into question the assumption that blue swimmer crab fisheries in Western Australia are robust to recruitment overfishing. It appears that high levels of fishing pressure, coupled with three years of reduced recruitment due to unfavourable environmental conditions, resulted in a significant reduction in the levels of egg production (Fig. 5). This reduction is evident after 2003/04 and these levels have remained low in subsequent years. High exploitation rates were exacerbated by a shift by commercial fishers in 1993/94 from set nets to crab traps coincided with a marked increase in average total crab landings by the late 1990s (D.J. Johnston et al. pers. comm.). The shift to crab traps resulted in an increase in the winter catch where there was high proportion of females caught. These females would have participated in their second year of spawning and their removal would have exacerbated the rate of decline in the EPI during periods of low recruitment.

Cockburn Sound is certainly not the first crab fishery thought erroneously to be resilient to overfishing. Chesapeake Bay blue crab fishery, once the most productive estuarine system in America, continues to report lower harvests each season since catches peaked in the early 1990s. These declines in catches are considered to be due to a combination of overfishing and adverse water quality and environmental conditions (Bunnell and Miller 2005, Lambert et. al. 2006a,b).

The SRR with environmental effects incorporated needs to be further tested because the time series of stock and recruitment data used to generate the relationship in this study is relatively short (only nine years). The key test should occur in the next few years as the fishery recovers. The time period for the recovery for this short-lived species is expected to be relatively fast (e.g., 3-4 years) especially with the favorable water temperatures recorded for 2006 and 2007. The recruitment-environment relationship also needs to be verified, as there are large numbers of environmental conditions that can be tested in space and
time; this raises the risk of spurious correlations (Walters and Collie 1988). In the present study the water temperature time series at the nearest location near the spawning and larval period was the only variable tested, as it was considered the key indicator likely to influence the crab stock.

The stock-recruitment-environment relationship produced during this study allows catch predictions to be made for the Cockburn Sound crab fishery a year in advance. This forecasting capacity can be verified by the abundance of juvenile crabs sampled in March-August (Bellchambers et al. 2006, D.J. Johnston et al. pers. comm.), reduces uncertainty for fisheries managers and enhances their ability to make sustainable management decisions. The early implementation of informed management actions significantly aids in the sustainable management of this fishery.

The development of an egg production index for Cockburn Sound provides managers with a baseline against which the level of *P. pelagicus* breeding stock can be assessed. However, these results demonstrate that, even at adequate levels of egg production, year to year variability in environmental conditions have a large influence on *P. pelagicus* recruitment. This variability is important to the resilience of the fishery and needs to be accounted for when developing robust biological trigger points (D.J. Johnston et al. pers. comm.). This model, which quantifies the influence of water temperature on crab recruitment, will aid in the management of the fishery.

It is worth considering the combination of factors that has contributed to the collapse of this seemingly robust stock to enable an assessment of whether other similar fisheries may also be vulnerable. For the Cockburn Sound crab stock the key factors were (a) the fishery is near the edge of this species distribution and hence vulnerable to environmental fluctuations; (b) a number of consecutive years of poor environmental conditions resulted in poor recruitments; and (c) high fishing pressure continued to be applied to the stocks.

There have been two other crustacean fisheries where recruitment overfishing has occurred in Western Australia in the 1980s—the tiger prawn (*Penaeus esculentus*) stocks in Exmouth Gulf and Shark Bay (Penn and Caputi 1986, Caputi et al. 1998). There are some similarities with the crab collapse, as the tiger prawn was also near the edge of its distribution with a restricted spawning period compared to other prawn stocks in the region and subject to large fluctuations in abundance due to environmental conditions. Its life cycle was also contained within embayments with the spawning stock aggregating in the deep water and hence vulnerable to fishing throughout the life cycle. While there was no change in fishing method associated with these fisheries, there were significant increases in fishing power of the vessels and the introduction of prawn peeling machines that enabled the prawns to be targeted...
earlier in the season at a much smaller size. The tiger prawn stocks had two additional factors that contributed to their overfishing that do not occur in the crab fishery. The multispecies nature of the prawn fishery resulted in the tiger prawn stocks being fished at low abundance level because of the good abundance of the king prawn stocks. Secondly, the tiger prawn stocks were fished for a number of months before spawning commenced whereas the crab stocks are fished after the first spawning of the year class is completed.

While the stock-recruitment-environment relationship produced during this study is unique to Portunus pelagicus in Cockburn Sound, the factors contributing to the collapse are directly relevant to other highly exploited fisheries, particularly those whose catches are based on a single age class, e.g., blue crab in Chesapeake Bay, and stocks that are near the limit of their species distribution, e.g., South Australian blue swimmer crab stocks and Florida spiny lobsters (Panulirus argus).

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